MINISTRY OF AGRICULTURE, FISHERIES AND FOOD

FISHERY INVESTIGATIONS

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The biology and distribution of the Slipper Limpet *Crepidula fornicata* in Essex Rivers

with notes on the distribution of the larger epi-benthic invertebrates

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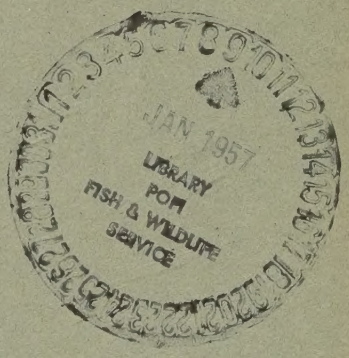

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Part I. Introduction and review of previous work

1. GENERAL

R over 50 years the presence of *Crepidula fornicata* on the coasts of Essex and Kent has n a matter of concern to oyster planters. The work reported in this paper was undertaken he Fisheries Laboratory, Burnham-on-Crouch, in order to increase our knowledge of habits of this species on Essex oyster beds. Without a full knowledge of its ecology it is icult to assess the damage it may do or to devise effective methods of control.

General accounts of the occurrence of *Crepidula* and its influence on English oyster s have been given by Murie (1911) and Orton (1912b, 1937).

The native distribution of *Crepidula fornicata* is on the eastern seaboard of the American tinent, from Escuminac Point, New Brunswick, (47°N.), and Summerside, Prince ward Island, in Canada, to the Caribbean islands of St. Thomas, Curacao, Cuba and rto Rico (18°N.) (information from the United States National Museum, Washington, C.). *Crepidula fornicata* has also been recorded from Uruguay (same authority), but not n Argentina (Parodiz 1939). From the east coast of the U.S.A. it has been carried to the ific (Chapman and Banner 1949) and to Northern Europe, where it is now found on t or all of the coasts of England, Wales, France, Belgium, Holland, Germany, Denmark Sweden.

Crepidula fornicata is colloquially known in this country as the American slipper limpet Bungalows' (part of Essex). The shell is oval and limpet-like, with a posterior apex, ch is twisted to one side and joined to the margin. The surface of the shell is fairly oth and of a light brownish-grey colour. In the younger stages it is marked with gitudinal light brown lines which become obscured in older specimens. The cavity of shell is divided posteriorly by a horizontal diaphragm which protects the visceral hump. e diaphragm occupies about half the aperture and is white; the inside of the shell is dish-brown.

A muscular yellow or orange foot covers the diaphragm, while the head and the opening he mantle cavity occupy the open part of the shell aperture. During the male phase nis, which is usually black, but may occasionally be yellow, is present on the right side he head. The dorsal surface of the animal, which is black or grey, is covered by the ntle cavity enclosing the large ctenidium. An account of the anatomy is given by Werner Grell (1950).

The younger slipper limpets are able to move freely, but after about two years old, the ver of locomotion is gradually lost (see below). By this time the slipper limpets have umulated into chains of individuals, each individual gripping tenaciously to the dorsal face of the shell of the subjacent partner in the chain. Conklin (1897, 1898) noticed that males and females were markedly dissimilar in size. Later Orton (1909) described how oldest and largest individuals at the bottom of a chain were females, while the younger smaller, individuals at the top of the chain were males. It was apparent that a change sex had taken place, and individuals in the intersex condition, where the penis was ressing and the uterus developing, were found in the middle of the chain. The primary

gonad of the young *Crepidula fornicata* is bi-sexual (Orton, 1909, Coe, 1935), and, at transition, there is a neuter period during which the remaining spermatogonia are cytoly and the oogonia develop.

This discovery initiated many studies of the factors influencing the time of the change in this and other species of the genus, especially by Gould (1917a, 1917b, 19 1947, 1952), Coe (1935, 1936, 1938a, 1938b, 1942a, 1942b, 1947, 1948a, 1948b, 1953) Ishiki (1936, 1939). It was found that if immature slipper limpets are cultured in associat with mature females, the great majority assume the functional male phase. If, howe immature specimens are cultured under similar conditions, but without the presence females, only about half develop into the functional male phase and the remainder beco functional females. A few of these females first develop partially into a non-functional m phase. It has been concluded (Gould, 1952, Coe, 1953) that these variations are due congenital differences in the tendency of individuals towards maleness or femalen Gould (1919, 1952) presents evidence to show that the formation and maintenance of male phase is influenced by a substance or substances secreted into the water by mat females and this view has recently been followed by Coe (1953).

Orton and Rogers (1950) and Orton (1952) reported finding isolated breeding fem on escallop shells from the English Channel and on mussels at Teignmouth, Devon, suggested that it is likely that these specimens were self-fertilised, but this hypothesis not yet been confirmed by laboratory experiments.

Conklin (1897) has described the process of cleavage and the formation of the germi layers and definitive organs in the embryo. The development of the larvae and th metamorphis has yet to be described; Lebour (1937) and Thorson (1946) each giv figure.

The eggs are laid in a bunch of capsules, each containing about 250 eggs. The capsu are attached to the substratum and are brooded by the parent. The embryos escape advanced veligers which are planktonic for about a month. The breeding period and duration of embryonic life in the river Blackwater have been investigated by Chipperfi (1951) who found that spawning commenced in April when the water temperature risen to 10°C., and continued until September. Hatching took place 21-28 days af spawning and most females spawned at least twice in a season.

The feeding mechanism has been described by Orton (1912a), Yonge (1938) Werner (1951). A large ciliated gill, the homologue of the ctenidium in non-filter-feed Gastropods, runs the length of the mantle cavity. The cilia cause a current to enter gill chamber on the left side of the head and to leave on the right side. Food particles in water are caught either by the mantle mucous filter, which stretches across the inhal current (Werner, 1951), or, failing that, by the gill which lies behind. The mantle muc filter is continuously drawn forward to the food pouch and then to the mouth. Parti trapped by the gills are deposited in a ciliated groove which runs along the right side of floor of the mantle cavity, food particles embedded in mucus pass forward along ciliated groove to the mouth where they are seized by the radula. During the mobile st a certain amount of grazing also takes place.

Associated with the filter feeding habit is a crystalline style (Orton, 1922), lying i sac partially separated from the intestine. The function and anatomy of this region clos resembles that of the analogous structures in lamellibranchs (Mackintosh, 1925). Wh slipper limpets are kept out of water for two days the style disappears but if kept in aera water and starved the style is maintained (Yonge, 1925).

2. *CREPIDULA FORNICATA* AS AN OYSTER PEST

The slipper limpet does not actively attack oysters. It is possible that it may beco sufficiently numerous to compete with oysters for food, but this has not yet been prov Korringa (1951a) states that on Dutch beds oysters fatten equally well whether *C. fornic* is present or absent. Chapman and Banner (1949), studying the mortality of *Ostrea lur* on the dyked beds of Puget Sound, found that there was no relationship between

ndance of *C. fornicata* and the condition of the oysters. Their mortality counts showed in general the more *Crepidula* that were present, the lower was the oyster mortality, they suggest that the slipper limpets were being adversely affected by the same factors ne oysters.

The presence of slipper limpets in quantity makes it more laborious to cultivate oyster nds in an effective manner. If the slipper limpets are allowed to remain,the continuous duction of faeces and pseudo-faeces leads to the accumulation of mud and the bottom mes soft and unsuited for oyster culture. The final result is the typical 'mud and ets' of derelict oyster grounds in Essex.

The shell of living oysters is frequently selected by young slipper limpets as a surface attachment (Verrill, 1873, Orton, 1926), and cause additional work in preparing the er for market.

There are other ways in which slipper limpets may have an adverse biological effect on ers. Korringa (1951b), has shown that the dead shells may become reservoirs of ction for a serious fungal disease of the shell of oysters. This fungus can spread from dead shells of *C. fornicata* to oysters, especially spat, with which they may be in contact, considerable loss can occur.

Although we have no detailed quantitative knowledge of the fauna of Essex oyster beds re the arrival of *C. fornicata*, it is probable that this species has, to a large degree, me an addition to the fauna, without supplanting other forms. There may well be gh food present to support such an increased population, but we do not know yet ch items of the plankton are most important for the growth of either slipper limpets or ers (Korringa, 1952a). It has, however, been shown that oyster larvae will only thrive certain constituents (Bruce, Knight and Parke, 1940), and Knight-Jones (1952) has gested that their growth in Essex estuaries may often be limited by the food supply. colleague, Mr. M. N. Mistakidis, tells me that the larvae of *C. fornicata* are usually as ndant as oyster larvae in the river Crouch; it is possible therefore that their presence ces the amount of food available for oyster larvae.

Korringa (1951a) notes that oyster larvae are swept in by the feeding current and sequently trapped in the food masses of *C. fornicata* and doubtless many are lost in way. Mature settling larvae of many species compete for the available surfaces and l which has been scattered to attract oyster spat, may, in fact, collect a spatfall of per limpets. Korringa recommends the use of mussel shell as cultch as this is more le than cockle shell. When the mussel shells break up, an attached oyster is set free out harm, but large limpets are unable to re-attach themselves if their substratum nbles. Loosanoff and Engle (1941) suggest that *C. fornicata* spat grow sufficiently fast in g Island Sound to smother oyster spat; Knight-Jones (1952), however, found them to nimportant as competitors in the rivers Roach and Crouch compared with barnacles and ozoa. Ingle (1951) places *C. fornicata* next to barnacles as competitors for settling space he coast of Florida.

3. UTILISATION OF *C. FORNICATA*

nidula is obtainable as a by-product of the oyster industry. Unfortunately the British lic is very conservative in its tastes and attempts to sell slipper limpets for human umption met with no success. In 1926, for example, a large firm of London shellfish chants offered them unsuccessfully at three shillings per bushel wholesale.

During the last two world wars, the increased attention given to available local raw erials resulted in *C. fornicata* being utilised for short periods. In the 1914-1918 war it processed for poultry grit in this country and in the 1939-1945 war it was used as a ce of protein in Holland.

At the beginning of the 1914-1918 war the Board of Agriculture and Fisheries (Ministry griculture and Fisheries, 1920) established a plant near West Mersea on the river kwater, for crushing slipper limpets which had been purchased from fishermen. crushed product was sold as a fertiliser. Although it was useful locally, it was too

bulky to transport any distance. Later in the war a small factory was established by th Board at West Mersea for the production of poultry grit. The slipper limpets were fir allowed to rot on the salt marshes, and when bleached, the shells were crushed to vario grades of grit. In the period 1916-1921, about 1,400 tons of the raw material were purchas annually from the fishermen for approximately 10 shillings per ton. This sufficed for a average annual production of 800 tons of grit which was sold for about £6 a ton. A sma profit was made, but in 1922 falling prices, the cheap importation of oyster shell as ballas cargo from America, and the Government policy of withdrawing from state tradin resulted in the closing down of this project.

The shortage of protein foods during the 1939-1945 war led the Liebig Company Holland to experiment with *C. fornicata* and eventually a paste was produced and succes fully marketed. During the war some 30 million kg. of slipper limpets were processed b the product was not successful when easier conditions returned (Korringa, 1952b). Th animal was not utilised in this country either during or after the recent war. Orton (194 appealed unsuccessfully for a state scheme as an aid to oyster fishermen as their groun had suffered serious neglect.

In 1950 the County Poultry Advisory Officer for Essex used slipper limpets suppli from the Fisheries Laboratory, Burnham-on-Crouch, as a protein food for poultry. Th experiment continued for seven months and showed that for egg production slipp limpets are a satisfactory source of protein; as, however, the dry weight of meat is on about 2·8 per cent of the original weight, the cost of preparation made their use uneconom

During the 1939-45 war an investigation was also made by the Developme Commission, in conjunction with the Ministry of Agriculture and Fisheries, of the pos bility of preparing a poultry meal from the mussel, *Mytilus edulis*. It was found that t chief problem was the high proportion of shell, the dry weight of the flesh being abo 7 per cent of the total fresh weight. Some experiments on a semi-commercial scale show that 12-30 tons of mussels, the amount depending on their condition, were required make 1 ton of meal; the meal contained 28 per cent protein. It was estimated that t mussels would cost about £2 a ton to collect and about £6 per ton of meal produced process. The finished product would therefore cost £30 to £60 a ton to prepare at the pric ruling then, and from this it was concluded that it would not be an economic proposition.

Owing to their lower meat content, the production of poultry meal from *C. fornica* would require the use of even larger quantities of raw material. Fresh slipper limpets the shell contain about 1·6 per cent protein (Table 6). An experiment on a laboratory sca by Mr. G. D. Waugh, at Burnham-on-Crouch, produced a meal containing 39·7 per ce protein and about 33 per cent shell. A ton of this meal could, if perfect extraction w accomplished, be obtained from about 25 tons of fresh limpets. Theoretically, if all t shell could be eliminated, a meal containing 57 per cent protein could be produced. It wou be necessary to process about 36 tons to produce a ton of meal.

Any shellfish meal would have to compete with fish meal. At the time of writi (summer, 1954) the delivered price of fish meal containing 50-60 per cent protein is abo £70 a ton. This meal is equal in protein content to the best that can theoretically produced from slipper limpets. In fact, it is unlikely that a meal could be produc containing more than 40-50 per cent protein and the possible return is likely to be abo £60 a ton. It therefore seems unlikely that more than a few shillings will be available f each ton of slipper limpets after the cost of processing, bagging and transporting ha been met and allowance has been made for capital charges. It appears that a perfe solution would also utilise the shells, as in the West Mersea scheme, since these constitu a very much larger proportion of the raw material.

Part II. Influence of temperature and salinity

Number of observations were made to determine the effect of temperature and, nity on the functioning of *Crepidula fornicata*. Feeding rate and survival were the ncipal criteria used in assessing the results of experiments.

1. TEMPERATURE

(a) Mortality after Freezing

e effect of freezing in air was investigated. Slipper limpets do not normally extend ve low water mark of ordinary neap tides and hence are exposed to the air only for short iods.

A sample of large slipper limpets was kept in aerated water in an unheated store for a days and was then exposed to the air on a tray in a refrigerator. At various intervals nples were removed from the tray and replaced in sea water of about 8°C. After 7 days samples were examined. In those samples in which mortality had occurred, the total nbers of live and dead limpets were counted (Table 1). A control sample was kept in air he store for the same length of time as the longest frozen sample. No mortality occurred his sample.

Table 1: *Mortality after freezing* C. fornicata *in air*

Duration of freezing	Temperature °C.	% Dead after 7 days
35 min.	− 6·0°	0
1 hr.	− 6·0°	0
2 hr. 15 min.	− 5·0°	0
4 hr. 30 min.	− 5·0°	1
6 hr. 30 min.	− 5·5°	29
12 hr. 20 min.	− 6·0°	92
34 hr.	− 6·0°	100
2 hr.	− 4·5°	0
4 hr.	− 4·0°	0
5 hr.	− 5·0°	0
9 hr. 10 min.	− 4·0°	10
24 hr.	− 6·0°	63

The mortality at − 5°C. to − 6°C. was more marked than that at − 4°C. to − 5°C., there was no mortality in either experiment until after about 4 hours exposure at these peratures. It is possible that a sharp frost, occurring at the time of low water, might ctly kill a proportion of those slipper limpets which had become established at low tide l. This effect would be more pronounced on young specimens which, having thinner lls and less volume, would cool more rapidly. Under natural conditions a hard frost also make the water colder than 8°C., and this may further hinder their recovery.

It is concluded from these experiments that *C. fornicata* is not particularly susceptible low temperatures and the mortality curves probably closely represent the time taken the tissues to become frozen. Allee (1919) notes that there was no change in the Woods H population of *C. fornicata* after the severe winter of 1917-18 when the water temperatu did not rise above 0·0°C. for 80 consecutive days.

Dodgson (1928) exposed some sub-littoral mussels (*Mytilus edulis*) to air frost in t open for 24 hours, during which period the temperature varied from − 6·1°C. to + 1·1° and remained below freezing for at least 18 hours. After 24 hours these mussels were plac in sea water but there were no survivors. These results agree with the results obtain from freezing *C. fornicata* at − 6°C. as these mussels were frozen for at least 18 ho and probably longer. Partial thawing only would have been produced by the no temperature of + 1·1°C.

Luyet and Gehenio (1938), in a review of death caused by low temperatures, conclu that most organisms, providing their vital functioning is not impaired, either die near t freezing point of their tissues or are able to withstand very low temperatures.

(b) Temperature and Feeding

(i) field observations

The intensity of feeding was observed in the river Roach in the winter of 1949-50. Wh *Crepidula fornicata* is kept of out water the contents of the gut are discharged as fae pellets and collect around the anus. This is contrary to the experience of Dodgson (192 with *Mytilus edulis*, who found that stored mussels never extruded faeces into the man cavity. The passage of food through the gut of filter feeders is often rapid. It has be shown that *Mytilus edulis*, (Dodgson, 1928) discharges its gut contents within a few ho of ingestion (at a temperature of 15°C.) and Loosanoff and Nomejko (1946) state that

Table 2: *The feeding of* Crepidula fornicata *in the river Roach.* (*For description of the method see p.* 7)

Date of capture	Date examined	Number discharging faeces	Number in sample	% Feeding	Mean temperature preceding three days
Dec. 2, 1949	Dec. 6, 1949	37	46	80·5	No record
,, 16, ,,	,, 22, ,,	35	54	64·9	5·2
,, 23, ,,	,, 29, ,,	26	46	56·6	4·4
,, 30, ,,	Jan. 5, 1950	21	41	51·2	6·4
Jan. 6, 1950	,, 11, ,,	29	44	66·0	6·4
,, 14, ,,	,, 18, ,,	39	70	55·8	6·6
,, 21, ,,	,, 28, ,,	33	100	33·0	2·9
,, 28, ,,	,, 31, ,,	26	97	26·8	1·0
Feb. 3, ,,	Feb. 7, ,,	5	47	10·6	3·0
,, 10, ,,	,, 17, ,,	18	41	44·0	4·8
,, 17, ,,	,, 21, ,,	37	39	95·0	6·3
,, 24, ,,	,, 27, ,,	46	57	80·6	6·9
Mar. 3, ,,	Mar. 7, ,,	31	46	67·5	4·9
,, 10, ,,	,, 15, ,,	26	29	89·6	7·5

C. food particles pass through the gut of *Gryphaea virginica* in one to two hours. ems probable that the discharge of faeces by *C. fornicata* in the winter months indicates ther or not the individual had been feeding in the preceding one or two days.

Samples of limpets were dredged each week from the river Roach (Fig. 19, Section 8) placed in an unheated store. After a few days, those individuals which had a shell th greater than 3 cm. were examined and the presence or absence of faeces recorded, ble 2). No attempt was made to estimate the abundance of faecal pellets. Over the perature range studied (1·1 C. to 7·5°C.) the percentage of slipper limpets feeding was ctly correlated with the mean water temperature on the day of collection and the two eding days, (Fig. 1). More than half the limpets were feeding at temperatures above ., and at temperatures above 7°C. the great majority.

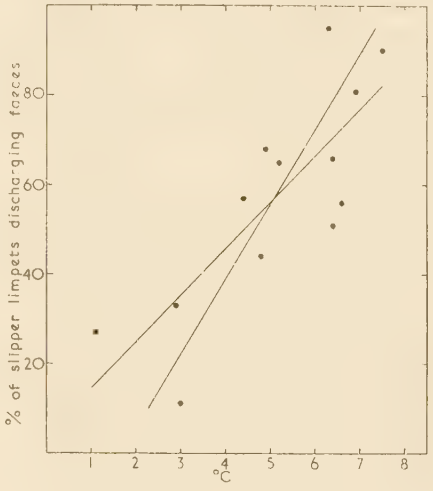


Fig. 1. *Feeding of* C. fornicata *in the River Roach during the winter of* 1948-49. *The percentage of individuals in weekly samples discharging faeces in the laboratory related to the mean water temperature for the preceding* 3 *days. The calculated regression lines are also shown.*

LABORATORY EXPERIMENTS

The rate of feeding was examined in two series of laboratory experiments in water of ous temperatures. Slipper limpets were dredged and immediately placed in sea water; ept in air for a short while, bubbles may be trapped in the mantle cavity and are not lily expelled. On reaching the laboratory the cleansed slipper limpets were placed in ls of aerated water. They were not otherwise disturbed or broken away from their chment. Several days acclimatisation were allowed before observations began. The nsity of the feeding current was estimated by observing the rate at which the vital ı, neutral red, was removed from the water. This method (Cole and Hepper, 1954) vs comparative differences in activity since the rate of removal of the dye is related to rate at which water is passed through the mantle cavity of the limpets.

Four drops of a 1 per cent solution of neutral red were added for each litre of water. en the dye was fully dispersed, 100 ml. were removed as the initial standard. After the uired period a further 100 ml. was removed, three drops of concentrated hydrochloric were added to each sample to intensify the colour and the two samples compared in ner cylinders.

In the first series of experiments three bowls were set up, each containing two litres a water and 12 limpets. Two were kept in an unheated store and one in the laboratory. r 7 days acclimatisation the activity of the feeding current was tested (Table 3). The ratory culture at 14·3°C. was found to be functioning a good deal more rapidly than duplicate store cultures which were tested at 8·3°C. The duplicate cultures agreed well.

In the second series, four bowls, each containing four litres of sea water and 20 limpets e set up. One bowl was kept in a heated laboratory, another in an unheated store and in a refrigerator where the temperature varied from + 0·5°C. to — 0·8°C. After days acclimatisation one of the two bowls was moved from the refrigerator to the ratory and after a further two days the feeding current was tested in all cultures.

Table 3: *The influence of temperature on the feeding current*

Date	No. of limpets and vol. of culture	Situation of culture	Acclimatization period	% Reduction of standard	Mean temperature °C.
19.12.49	12 in 2 l.	Laboratory	7 days	56*	14·3
19.12.49	12 in 2 l. (in duplicate)	Store	7 days	28*, 32*	8·3
12.3.50	20 in 4 l.	Laboratory	15 days	93†	14·1
12.3.50	20 in 4 l.	Laboratory (after 13 days in refrigerator)	15 days	72†	15·3
12.3.50	20 in 4 l.	Unheated Store	15 days	70†	10·2
12.3.50	20 in 4 l.	Unheated Store	15 days	19†	0·1

*After 1½ hrs.
†After 4 hrs.

The slipper limpets received no food or change of water during the acclimatisation perio The results (Table 3) again show the considerable dependence of the feeding current the temperature.

(iii) ACTIVITY OF THE GILL CILIA

Some observations were made of the rate of movement of small particles placed on gill. If the head and propodium are cut away with scissors, in a slipper limpet which been left in its shell, about half the gill is exposed. This avoids disturbance of the gill, a by placing the slipper limpet, ventral side uppermost, in sea water, the gill can be obser under a binocular microscope. Fine carborundum powder was allowed to fall on to t gill and the time taken for a particle to be moved by the frontal cilia over a distance meas by an eyepiece micrometer was noted with a stopwatch and the temperature record The activity of the cilia in a preparation was undiminished after many hours, but, a about 30 trials, the filaments of the gill start to separate; the structure is not so rigid a analogous organ in many lamellibranchs.

The results from 8 slipper limpets have been averaged at intervals of 1°C., and plotted in Fig. 2. The speeds of movement of small particles obtained in these experim

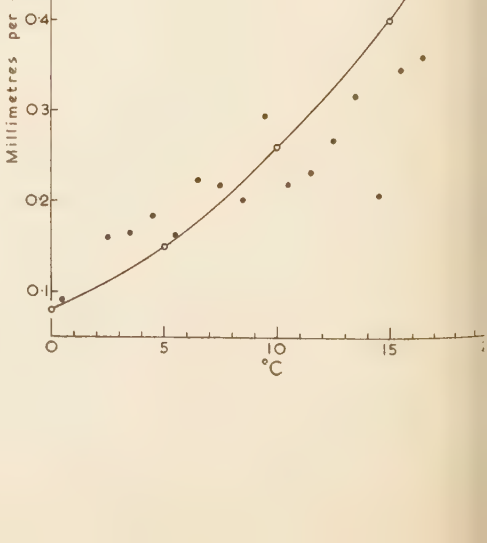


Fig. 2. *The rate of movement of carborundum particles by the gill cilia of* C. fornicata *related to temperature. The curve shown is the rate of movement of a platinum disc by the gill cilia of* Mytilus edulis (*from Gray*, 1928).

similar to those obtained from *Mytilus* (Gray, 1928). The feeding rate is directly related temperature as in mussels and other lamellibranchs.

2. SALINITY

(a) Toleration of Reduced Salinity

8.1.49, five glass vessels, each holding 15 litres of water, were set up. The salinity of the r in different vessels varied from 34‰ to 25·2‰ and they were stood in an unlit and eated store. A few chains of slipper limpets were hung in each vessel by threads ched to the proximal ends of the chains in the hope that as the limpets weakened, due to vourable conditions, the chains would part. In the next two months, however, only chains parted, one in the jar at 25·2‰, the other in the jar at 34‰, and no limpets . Three weeks after setting up the experiment, the activity of the gill cilia was examined ndividuals from the jars of the lowest and the highest salinities used, by observing the d of carborundum particles according to the method already described, but no rence in activity could be seen. When the chains were tested on 8.3.49 it was clear n the effort required to pull the chains apart that those limpets which had been in water alinity 25·2‰ were distinctly weaker. Nevertheless, the experiment shows that slipper pets will survive for considerable periods in moderately reduced salinities. In fact, pman and Banner (1949) have shown that *C. fornicata* can become established in areas ermanently reduced salinity. These authors record up to 178 per square foot in oyster es in Mud Bay on the south side of Puget Sound where the annual salinity range is 28·5‰ (Hopkins, 1937). The maximum shell length in a random sample from one

Table 4: *The influence of salinity on the feeding current*

Date	15.11.49		15.11.49		25.11.49		25.11.49	
Hours acclimatization	140		140		144		144	
Litres per culture	4		1		5		4	
Limpets per culture	12		3		15		12	
Temperature range °C.	13·4 – 14·2		13·4 – 14·2		13·5 – 14·5		13·5 – 14·5	
Salinity	% Reduction of standard in 4½ hrs.	Av. shell length	% Reduction of standard in 4½ hrs.	Av. shell length	% Reduction of standard in 5 hrs.	Av. shell length	% Reduction of standard in 5 hrs.	Av. shell length
33·9	–	–	–	–	66	44·0	–	–
33·5	74	43·8	93; 88	50·3; 45·0	–	–	–	–
29·3	–	–	–	–	–	–	82	43·6
29·0	50; 66	44·6; 45·5	76	48·3	–	–	–	–
27·6	–	–	–	–	–	–	56	43·0
24·3	–	–	–	–	34	42·2	32	43·1
24·0	20	46·5	13	44·3	–	–	–	–
19·7	–	–	–	–	–	–	26	43·8

of the dykes in Mud Bay was 39·8 mm. (C. E. Lindsay, private communication). This only a little smaller than that found in many Essex populations.

(b) Salinity and the Feeding Current

Table 4 summarises some observations of the activity of the feeding current, measured the neutral red technique, in water of different salinities. The various salinities we produced by mixing waters collected from different parts of the river Crouch. Silt w allowed to settle out before use.

These four experiments showed that *C. fornicata* is sensitive to moderate changes salinity; a reduction from 33‰ to 29‰ produced a marked effect. At 24‰ a ve considerable reduction in the feeding current occurred.

In Essex, *Crepidula* is living in the more northerly part of its range and yet the influen of temperature on feeding is similar to that found in *Mytilus edulis*. Comparison wi *Mytilus* is invited by the amount of information which is available on this species and the knowledge that it is a hardy form found both on open coasts and in estuaries. Its hab are analogous to those of *C. fornicata*. In Britain *Mytilus* is approaching the more southe limits of its range so that one might expect to find it more resistant to cold than *Crepidu* In fact, resistance to air frost is similar in the two species and is apparently correlated wi the time taken for the tissues to freeze.

Part III. Growth

Oyster fishermen have claimed that slipper limpets multiply and grow so rapidly tha neglected ground may be overrun within two years. Considerable importance attach therefore, to a knowledge of its growth-rate under natural conditions in relation to t development of methods of control. Most of the information given below has been obtai from a detailed study of individual growth-rate in a population of slipper limpets on ground (Creeksea, Section 8) in the river Crouch.

1. SHELL SHAPE AND THE SHELL AND MEAT WEIGHTS

The proportions of the shell vary, the shape being influenced by the substratum and t space available for growth. Since most slipper limpets are members of chains, the sha of the shell of such slipper limpets can be taken as the typical one.

Fig. 3 shows the height and width of typical shells related to the length, from t combined random samples of chains fished at the standard station at Creeksea (see p. 1 Fig. 4 shows the axes which have been used for the measurement of the shell.

The height of the shell appears to be directly related to the length whereas the wid is apparently related to the length exponentially. In growth, new shell is laid down alo the margin and the diaphragm comes to lie deeper within the shell. The slight spiral tw is also maintained and the lateral attachment of the diaphragm is further from the right ha than from the left hand margin.

In this work, the length of the shell has been taken as the measurement of size, as th measurement may be made quickly and accurately. In consequence of the increase in t curvature of the shell with increase in size, i.e. a decrease in the length-height ratio, t same length of new growth laid down at the lip of the shell will have less effect on t length in the larger than in the smaller limpets. The unsatisfactory nature of a line measurement is further displayed by the curves relating the dry weights of the shell a the meat to the shell length (Fig. 3). At the larger sizes there are considerable increases the weight of the shell and the meat for small increases in length. The larger slipp

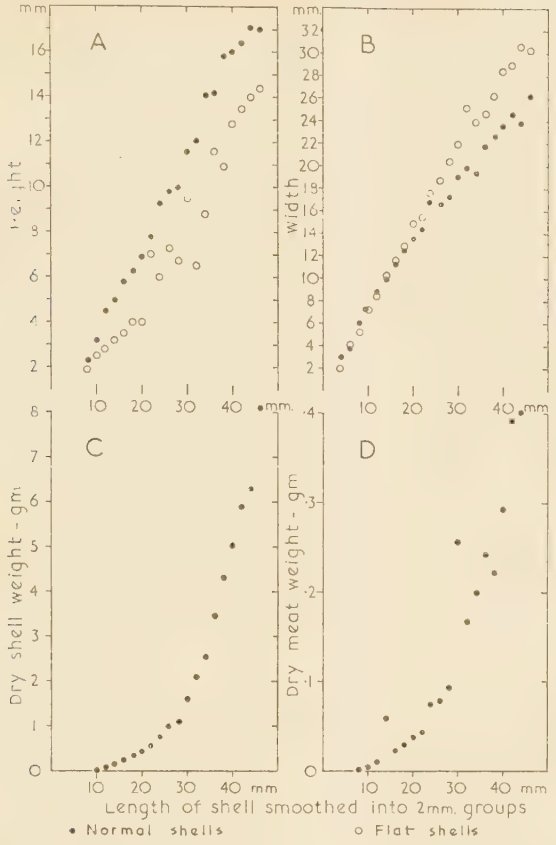


Fig.3. *Shape and weight of* C. fornicata. *The closed circles represent individuals from free clusters at Creek-sea (Sect. 8, river Crouch). The open circles represent a mixed collection of flat individuals growing on oyster shells in the Crouch and Roach.*

(A) Relation between height and length of shell.
(B) Relation between width and length of shell.
(C) Relation between dry shell weight and length of shell.
(D) Relation between dry meat weight and length of shell.

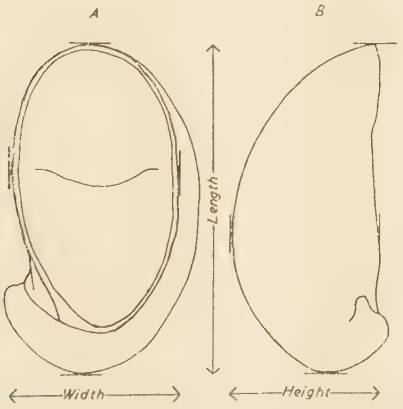


Fig.4. *The shell of* C. fornicata *showing the principal axes of measurement. A, ventral view. B, side view.*

limpets of a chain which are at, or near, the maximum size attained at a particular stati (see p. 24), also show a more rapid thickening of the shell (Fig. 3).

In a random sample of chains, female slipper limpets tend to have heavier shells th males of the same size. This is because the females are generally lower down a chain (a hence older) than males of comparable size, and the weight has increased by thickeni of the shell.

The divergence of shape from the typical is either in the direction of strongly curv or flattened shells. The former are only occasionally found, usually on small pebbl The latter type is more common, since this form of growth is induced by a flat surfac e.g. oyster shells. The mean height and width related to the length of a collection flattened shells is shown in Fig. 3. The divergence from the typical in the height becom marked at 10 mm., but the width of the shell is not affected to the same extent and appreciable divergence is not apparent until a length of about 28 mm. is reached. Amo large limpets of the same size, there is a greater range of shell weight in the flat-shell than in the typical form (Table 5). These large flat limpets have apparently grown quick to about the full size and have then increased in weight by thickening of the shell.

Table 5: *Range of shell weight in flat and normal-shaped slipper limpet shells*

Length of shell mm.	Weight of dry shell — gm.	
	Flat shell	Normal shell
45 – 46	4·0 – 10·9	6·3 – 8·7
43 – 44	3·6 – 9·1	5·6 – 8·8
41 – 42	1·9 – 10·5	4·2 – 8·1
39 – 40	2·3 – 8·7	4·4 – 7·5
37 – 38	2·1 – 4·5	3·4 – 6·4
35 – 36	2·0 – 4·1	2·9 – 4·4

An analysis by the Government Chemist showed that the shells contained 96·6 per c calcium carbonate, mainly in the form of aragonite. An analysis of the flesh made by t Essex Institute of Agriculture, Chelmsford, is given in Table 6.

Table 6: *Analysis of slipper limpet meat made by the Essex Institute of Agriculture*

	Fresh meat %	Dry meat %
Water	86·0	–
Protein	8·0	57·4
Oil	0·4	2·9
Sand, etc.	0·2	1·1
Silica free ash	2·8	20·3
Ca0	0·39	2·75
$P_2 0_5$	0·35	2·56
$K_2 0$	0·19	1·36
Chlorides as NaCl.	0·78	5·6

2. RATE OF GROWTH

(a) Introduction

on (1909) suggested that there is an annual increment of one slipper limpet on the end chain; he made a few observations of growth rate in 1913 (Orton, 1914). In the rivers kwater and Roach, Orton (1950) found that by August 1945 the slipper limpets from 1944 spatfall had reached 15-20 mm. In the English Channel, (Orton and Rogers, 1950) et spat ranged from 4-12 mm. by the first winter (see also page 23 of this paper).

Werner (1948) measured the size of spat which had settled on a number of floating cts in the Nordfriesischen Wattenmeer, the maximum sizes varied from 5·7 mm. after lays to 14·3 mm. after 56 days. Coe (1942b) gives a brief outline of the growth rate in ecies of *Crepidula*. He states that on the New England coast young spat change to the ale phase in the second summer at a size of 18 to 28 mm. Isolated individuals, however, h a length of 28 mm. in 6 months, if hatched in May. He observed a decrease in growth- during the functional sex phases and a sharp increase during the sex-change. In an ier paper (Coe, 1936), the measurements of several chains show that the sex-change irs at Woods Hole at about the same size as in Essex. One female of 30 mm. was found, remaining 17 females measuring 33-43 mm. In Florida, where the water temperature between 25° and 30°C. *C. fornicata* grew to 24 mm. in 5 weeks (Ingle, 1951).

(b) Method

idula fornicata is mostly sub-littoral. A study of the growth-rate, by recovery of marked imens by dredging would be very difficult, especially in areas where there is a dense ulation, and it is in such areas that interest centres. The study of the growth of marked imens which are confined in some way overcomes these disadvantages, but the atural habitat may affect their growth-rate.

There is no reliable marking on the shell of *C. fornicata* which could be used as an cation of annual growth, although growth rings can often be denoted on free living imens (Orton and Rogers, 1950). The dominant mark on the shell of individuals from ns is the scar caused by the foot and the edge of the shell of the slipper limpet attached ie dorsal surface of the shell.

In this investigation the growth of slipper limpets has been observed in detail during ral years at one station (Creeksea), in the river Crouch, by measuring samples and nining the movement of the modes. Samples have also been taken for comparative oses from other stations in the rivers Crouch, Roach and Blackwater.

As shown earlier, there is much variety in the growth forms of *C. fornicata*. Since most ie population is made up of limpets in clusters which are lying free on the bottom, and e slipper limpets show the minimum of shell variation, it was decided to restrict the rvations on the growth rate to individuals in such clusters.

A series of slipper limpets, each attached in the normal position to the dorsal side of its ner is referred to as a 'chain'. A chain may be attached to stones, shells, etc., or it may ying free on the bottom.It may also be attached to the side of another chain, in which it is referred to as a side-chain attached to a main chain. A main chain with its ched side-chains is referred to as a cluster.

The length measurement data have been smoothed into 2 mm. groups and each group ted as the percentage frequency of the entire sample. This gives a reasonably smooth e without disguising the position of the principal modes.

(c) Observations

size frequency curves were always of the same general shape. It is clear that up to it 30 mm. in length, the slipper limpet grows fairly steadily and this part of the curve made up of several peaks each representing a year class. These were the year classes

whose growth rate could be observed by studying successive samples. Further, as limpe below 30 mm. were usually still in the male phase, their growth would have been unaffect by sex change.

Above 30 mm. there was a broad curve which represented the adult part of t population. It was impossible to split this part of the curve into its constituent year classe In examining the samples it was occasionally found that the proximal one or two slipp limpets, and hence the oldest members, of the chain, were somewhat smaller than tho in the middle of the chain. In other cases several adult limpets of the same size would found adjacent in one chain, although adjacent small limpets differed in size. Clearly, si was no criterion of age in these adults; their growth had been modified by the limitatio of the substratum. The parts of the size frequency curves beyond 30 mm. represent number of closely over-lapping year classes.

1. GROWTH AT CREEKSEA

(*a*) *General*

This station, in Section 8 of the estuary of the river Crouch (Fig. 19), was convenien situated close to Burnham-on-Crouch, and carried an abundant slipper limpet populati lying on a muddy bottom. This type of bottom reduces errors which might occur due to t immigration or emigration of the mobile stages on and off the chains. As slipper limp require a firm substratum any movement that occurred would only be from chain to cha This would make no net difference to the sample. The depth at this station was ab 7 metres at low tide and the ground had been little disturbed by cultivation in recent yea Slipper limpets were first recorded from this laying in 1893 (Crouch, 1893).

39 samples were taken at intervals from May 1949 to November 1951. These were u to study the appearance of each year group and its subsequent growth. This series samples, in which a total of 15,999 slipper limpets were measured, gave the necessary in mation to give confidence in interpreting the length frequency curves. In addition, sam have been examined during each winter from 1947/48 to 1953/54 to observe the abund of juveniles.

Fig. 5 shows graphs from the main series of 39 samples. For brevity, when more th one sample was measured in any one calendar month, they have been combined and treated as one. Fig. 5 shows clearly the appearance of the newly metamorphosed sli limpets in the summers of 1949 and 1950. The 1949 spatfall can be judged, from appearance of slipper limpets in the 1-2 mm. group, to have lasted from the end of J until August. This spatfall gives a fairly broad peak whereas in 1950 the spatfall was r intense and occurred only at the end of June and in early July. This led to a sharply defi and narrow peak which can be followed through several years.

These graphs show that a study of the growth-rate of a year-class, at different tim of the year, can best be made during the growing season after the one in which the gro settled.

Each of the samples has been plotted on a large scale and the position of the mode the 1949 class in 1950, and of the 1950 class in 1951, has been read off to give the growt rate in the season following settlement. These data have been plotted in Figs. 6a and which show the size range of the year-classes as well as the position of the mode in each the samples.

The 1949 class started the 1950 growing season with a mode at 8 mm. and ranged length from 4 to 12 mm. By the end of the growing season the mode was at 14 mm. and t group ranged from 10 to about 22 mm. The 1950 class started its second growing seas at a rather smaller size, the mode being at 4 mm. and the range 2-8 mm. By the end the growing season the mode was at 12 mm. and the group ranged from 6 to 22 mm.

In Fig. 6c the position of the mode for each of these two year-classes (1949 and 19 in their second growing season has been plotted, for each of the samples, as a percenta of the season's growth which the limpets of peak size had made at the time of samplin Growth was slower in the spring of 1951 than in 1950. This was probably correlated w the water temperature; the mean temperature for March was 3°C. lower in 1951 than 19

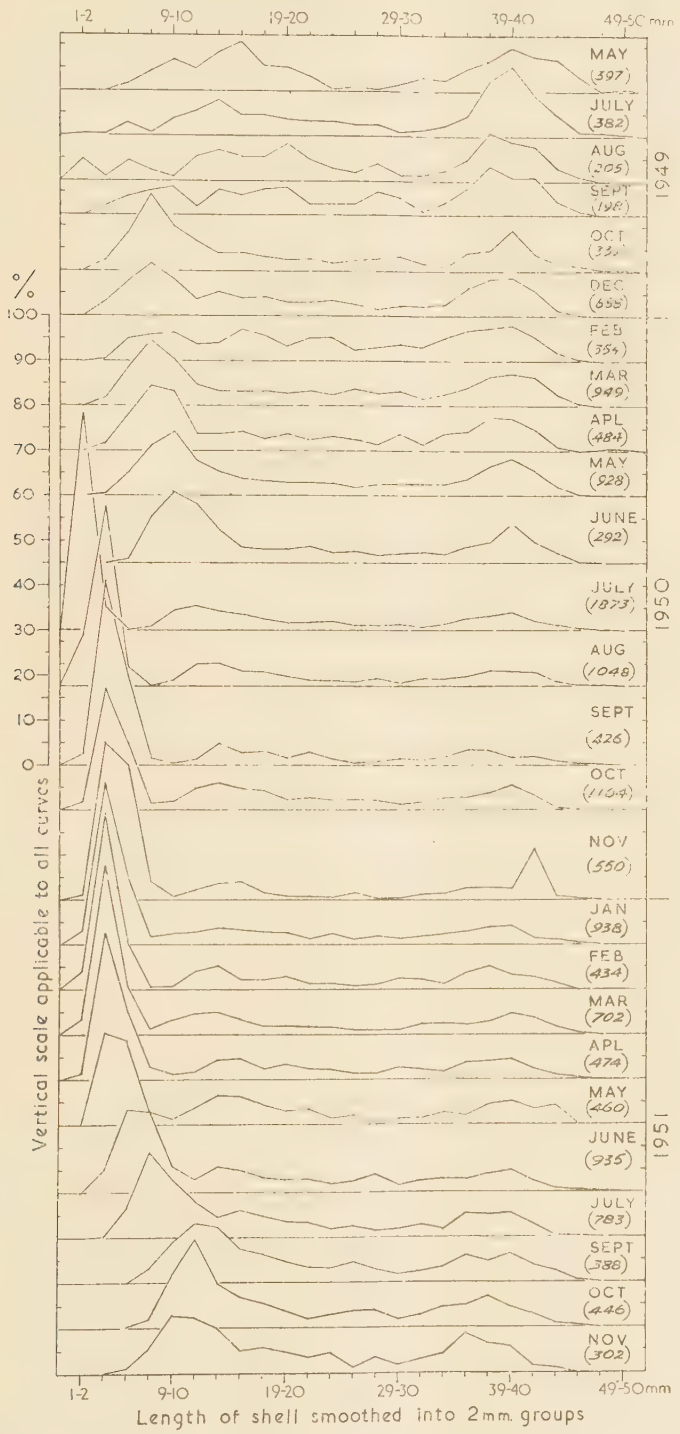


Fig.5. *The percentage size-composition of the population of* C. fornicata *at a station at Creeksea* (*Sect.* 8) *in the estuary of the Crouch. All graphs are drawn to the same vertical scale.*

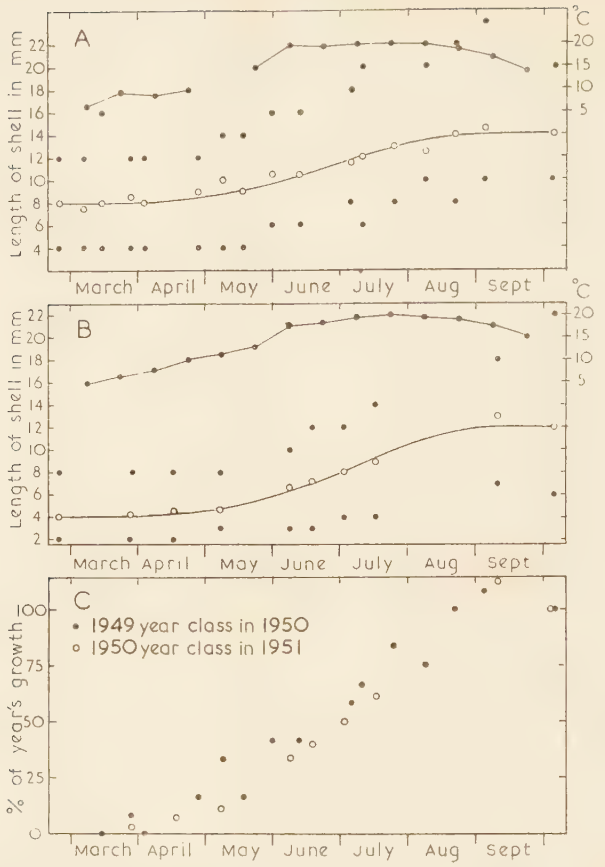


Fig.6. *The growth rate of* C. fornicata *in the estuary of the Crouch in the year after metamorphosis. The size range is shown by the two sets of dots and the mode by the open circles. In A and B the mean half-monthly water temperature is also shown.*

(A) Growth of the 1949 year group in 1950.
(B) Growth of the 1950 year group in 1951.
(C) Percentage of the total annual growth which had been made at intervals during the year.

In both years about half the annual growth was made in the two months June and July, th remaining half being spread over the five months March, April, May, August an September.

A general rise of water temperature in spring stimulates the commencement of growt and a general fall of temperature in the autumn stops further growth, but the growth-rat is not similarly correlated with the water temperature at all seasons of the year. She growth becomes appreciable in the spring when the mean water temperature rises to abou 8 C., whereas shell growth stops in September when the temperature is starting to fa fairly rapidly, but is still about 15°C.

Fig. 7 shows the size composition of the Creeksea stock in each winter from 1947-4 to 1953-54. It has been shown above that no growth occurs during the months fron October to February and so all samples taken in the course of a winter can be combinec A study of the graphs shows that in three of the years concerned, 1947, 1949 and 195(there was a fairly abundant and distinct spatfall. In the other years, 1948, 1951 and 195 the settlement was too sparse to appear as a distinct peak.

Two of the spatfalls can be followed into their second winter, and the third, that o 1950, can be followed into its third winter. An inspection of Figs. 5 and 7 shows that th

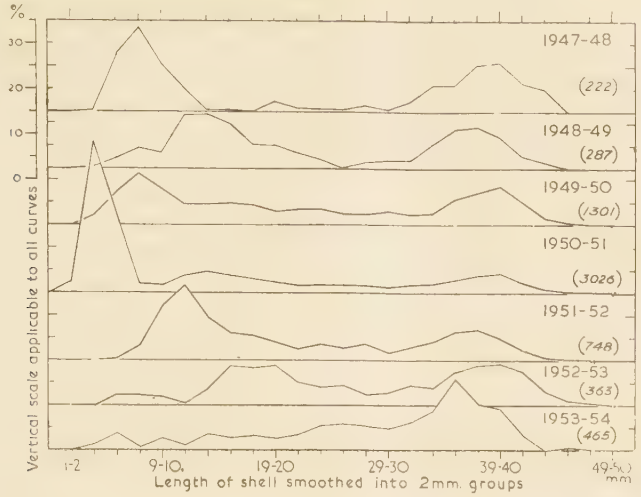


Fig. 7. *The percentage size-composition of the population at Creeksea in each of seven consecutive winters. The same vertical scale is applicable to all graphs. The numbers in the samples are shown in brackets.*

k size and range of three separate year-groups of slipper limpets at Creeksea in the ıter months were as follows:

	1947 year-class	1949 year-class	1950 year-class
e in first winter	8, (4-14)	8, (4-12)	4, (2-8)
e in second winter ..	14, (10-22)	14, (10-20)	12, (6-22)
e in third winter ..	—	—	18, (12-28)

The 1950 year-class was smaller at the end of its first growing season than the other ses so that the position of the mode in subsequent winters is lower than might be ected.

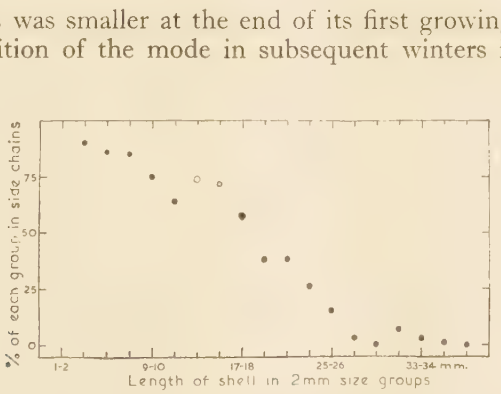


Fig. 8. *The percentage of each size group located in side chains. From random samples of clusters, Creeksea, winter,* 1949-50. (*Total* 1,301 *slipper limpets*).

The difficulties of interpreting the size-frequency curves above 30 mm. are accentuated a special mortality to which slipper limpets on chains are liable when approaching this . This special mortality is brought about by the lack of space available to side-chains. a free chain, slipper limpets can occupy two positions. They can either be members he main chain or alternatively they can be attached at various points on the side of the n chain, or as individuals making small side-chains. Those which are not in the main in are generally small, a point which is made clear by Fig. 8 which shows, for the ıbined winter samples from Creeksea for 1949-50, the percentage of each size group ch were not members of the main chain.

In a year of average spatfall, the terminal position in the main chain is quickly occupie so that the many small slipper limpets which are dotted about on the sides of a chain ha little hope of finding a position in the main chain while they are still mobile. The numbe of these slipper limpets falls off rapidly above about 16 mm. and none were found larg than 36 mm. An examination of a chain of slipper limpets shows that there is rarely roo for a slipper limpet of about 25 mm. to attach itself to the side of a chain without ove lapping two adjacent slipper limpets. This would be an impossible position, as the openi and closing of the two large slipper limpets would prevent the smaller from getting a fir hold and effectively closing. Slipper limpets in this position, therefore, either have to lea the chain or stop growing. If growth stopped, owing to the restricted space, an abundan of slipper limpets in the 30-35 mm. group, would be expected in the samples; slipp limpets of the same size but different ages. As the reverse is in fact the case, it is appare that those in this position are in some way leaving the sample after reaching about 20 m in size.

Those individuals which are members of a side-chain and are 16-26 mm. in size c leave the sample either by dying or by migrating off the free chain on to stones, shells, e These possibilities were examined by taking some samples with a Petersen bottom sampl at Creeksea. Three stations were chosen, A, B and C. C was identical with the routi sampling station and B and A were 75 metres and 150 metres further upstream respectivel Twenty samples, each of 0·1 sq. metre, were taken at each station. The overwhelmi preponderance of free chains (Table 7), compared with chains attached to stones, or she made it clear that the small side-chains and the individual slipper limpets were n

Table 7: *Analysis of slipper limpet population obtained from three stations at Creeksea, Ri Crouch, 3rd March,* 1949. *Each station covers* 2 *sq. metres*

	Free chains			Attached chains			Total limpets in 2 sq. metre
	No. of chains	Av. number per chain	Range	No. of chains	Av. number per chain	Range	
A	59	4·6	1 – 11	4	2·75	1 – 4	281
B	31	4·3	1 – 11	1	3·0	3	136
C	208	5·8	1 – 16	4	3·25	1 – 6	1235

migrating to stones and shells. The general appearance and fit of the shell of the first l limpet in the free chains showed also that the side-chains were not migrating to d shells. In fact, dead slipper limpet shells are by no means common on, or near, the surfa of the mud below low water mark. Those limpets which are attached to the side of a ma

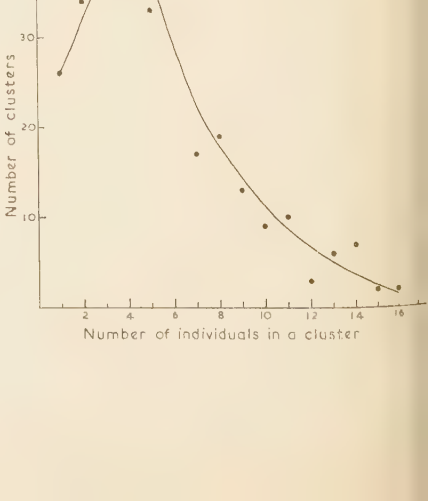


Fig.9. *The size-distribution of* 298 *free clusters found at three grab stations at Creeksea, (see Table* 6).

in apparently speedily die once growth stops as a result of the restricted space. If the vidual had already formed the base for a small side-chain, its death would start another chain.

In Fig. 9 the numbers of each size of cluster obtained from these 3 stations are plotted. e comparative abundance of small clusters in this well established population suggests free chains are being formed quite rapidly all the time, many of them undoubtedly ting as small side-chains.

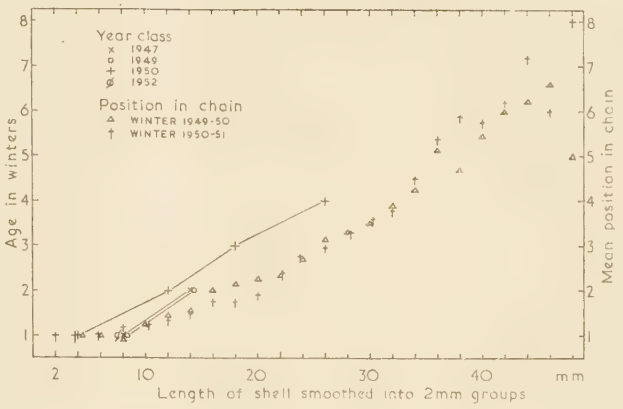


Fig. 10. *The position of the mode of four year-groups of* C. fornicata *for several winters after metamorphosis at Creeksea. The mean position in the chain of the various sizes is also shown for the Creeksea population in the winter of* 1949-50 *and* 1950-51. *Both sets of curves give an approximate estimate of the age of the larger individuals.*

Length at age

In Fig. 10 the modal sizes of the 1947, 1949, 1950 and 1952 year-classes are summarized as many successive winters as can be satisfactorily determined by inspection of the th-frequency graphs. This graph gives, by extrapolation, a means of determining the roximate age of the larger slipper limpets. The graph suggests that a size of about cm. is reached in the 6th summer.

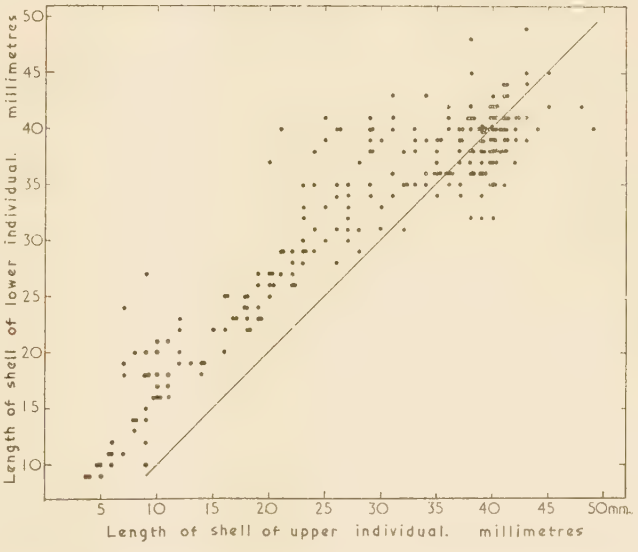


Fig. 11. *The relation, in free chains, between the size of shell of* C. fornicata *and the size of individuals attached to the dorsal surface. Each dot shows the lengths of the shells of two adjacent individuals from* 35 *chains selected at random at Creeksea in the winter of* 1949-50. *The curve represents the case of adjacent individuals of identical size.*

Confirmation of this estimate of the age of the larger slipper limpets is provided by idering the position of limpets of this size in the chains. An examination of the sizes djacent slipper limpets in the main chains (Fig. 11) showed that there was generally it 6 mm. difference in size between adjacent slipper limpets up to a size of about 3 cm., which the interval decreased and was sometimes negative, when the older slipper et was smaller than the younger. This latter effect results from restrictions caused by

the substratum to which the chain was originally attached. The presence of some adjacen individuals of similar size suggests that the usual size difference of adjacent slipper limpet is not controlled by a restriction imposed by the substratum but by the different ages c adjacent slipper limpets.

The approximate difference of 6 mm. in size between adjacent slipper limpets is of th same order as the known annual growth up to sizes of 3 cm. (see p. 19). Further, a examination of the average position of slipper limpets up to 3 cm. in size in the chai confirmed the hypothesis that about one slipper limpet was added to a chain each year.

Table 8: *Creeksea. Position in the main chain, related to length of shell, in the samples obtaine in the winters of* 1949-50 *and* 1950-51. *The position is counted from the youngest end.*

Length mm.	Position in chain									Mean position in chain
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	
1949 – 1950										
47 – 48	–	–	–	–	1	–	–	–	–	5·0
45 – 46	–	–	–	1	1	–	2	1	1	6·6
43 – 44	–	–	1	1	4	3	3	3	1	6·2
41 – 42	–	–	1	7	12	8	8	4	4	6·0
39 – 40	1	2	3	12	15	13	12	5	3	5·5
37 – 38	–	1	6	17	11	8	3	1	–	4·7
35 – 36	–	1	5	10	10	13	5	2	–	5·1
33 – 34	–	1	7	2	6	4	–	–	–	4·3
31 – 32	–	2	8	8	7	1	–	–	–	3·9
29 – 30	1	7	9	9	9	1	–	–	–	3·5
27 – 28	–	10	6	11	4	–	–	–	–	3·3
25 – 26	–	7	12	7	2	–	–	–	–	3·1
23 – 24	4	9	13	7	–	–	–	–	–	2·7
21 – 22	10	11	11	4	–	–	–	–	–	2·3
19 – 20	4	13	7	2	–	–	–	–	–	2·3
17 – 18	3	12	6	–	–	–	–	–	–	2·1
15 – 16	4	9	5	–	–	–	–	–	–	2·1
13 – 14	7	9	–	–	–	–	–	–	–	1·6
11 – 12	12	10	–	–	–	–	–	–	–	1·5
9 – 10	21	7	–	–	–	–	–	–	–	1·3
7 – 8	19	–	–	–	–	–	–	–	–	1·0
5 – 6	14	–	–	–	–	–	–	–	–	1·0
3 – 4	2	–	–	–	–	–	–	–	–	1·0
1950 – 1951										
47 – 48	–	–	–	–	–	–	–	1	–	8·0
45 – 46	–	–	–	–	1	–	1	–	–	6·0
43 – 44	–	–	–	4	–	4	6	5	2*	7·2
41 – 42	–	1	3	2	5	13	13	6	2	6·2
39 – 40	–	4	4	8	13	26	10	6	4†	5·8
37 – 38	–	–	2	7	15	8	14	7	–	5·9
35 – 36	–	–	3	7	17	12	6	2	–	5·4
33 – 34	–	4	4	15	18	8	1	–	–	4·5
31 – 32	–	3	11	20	6	1	–	–	–	3·8
29 – 30	–	3	13	12	4	1	–	–	–	3·6
27 – 28	2	3	13	15	1	–	–	–	–	3·3
25 – 26	1	8	14	5	2	–	–	–	–	3·0
23 – 24	–	9	16	1	–	–	–	–	–	2·8
21 – 22	2	6	9	–	–	–	–	–	–	2·4
19 – 20	6	15	4	–	–	–	–	–	–	1·9
17 – 18	11	13	4	–	–	–	–	–	–	1·8
15 – 16	9	17	2	–	–	–	–	–	–	1·8
13 – 14	11	11	–	–	–	–	–	–	–	1·5
11 – 12	4	2	–	–	–	–	–	–	–	1·3
9 – 10	3	1	–	–	–	–	–	–	–	1·3
7 – 8	5	1	–	–	–	–	–	–	–	1·2
5 – 6	31	1	–	–	–	–	–	–	–	1·0
3 – 4	14	–	–	–	–	–	–	–	–	1·0
1 – 2	4	–	–	–	–	–	–	–	–	1·0

*Also at the 10th, 11th and 12th positions.
†At the 10th position.

102 chains were measured in the combined samples from Creeksea obtained in the ter of 1949-50, and 103 chains from the similar samples of the 1950-51 winter. The size each slipper limpet was noted with respect to its position relative to the youngest end he chain (Table 8). Where a slipper limpet was separated from the youngest end of the in by an individual or individuals larger than itself, then it was assumed that its growth l been checked in some way, generally by the substratum, and it was ignored for the sent purpose.

The results, which are condensed in Table 8, show a steady increase in the minimum of slipper limpets found in each position, but occasional specimens of the larger pets are found in any position. This is because some individuals of all sizes die from one se or another. This causes a break in a chain and the larger individuals of the older half the chain are brought nearer to the growing end than their age warrants. This factor l bring the mean position of the larger slipper limpets to a lower position than would be case if death was confined to the oldest slipper limpets in the chains.

Using the hypothesis that, on the average, one slipper limpet is added to a chain each r, the mean position of each size group has been plotted in Fig. 10 where it is compared h the length-at-age curve obtained from the size-frequency data. There is fairly good eement between the two curves, although the chain-position curve lies a little to the t of the length-at-age curve. It is unlikely that the extrapolated length-at-age curve uld bend in this direction since it implies an increased growth-rate in the larger slipper pets.

There are two factors which will displace the position-at-age curve to the right. The t, that of occasional mortality breaking the chains, has been dealt with above. The second sibility is that the assumption that an average of one slipper limpet is added to a chain h year, is not quite correct. If, on the average slightly less than one slipper limpet is led yearly to each chain, then the curve will be displaced to the left. In this case, the umption of an average addition of about 0·8 slipper limpets added to a chain each year l make the length-at-age and the position-at-age curves coincide.

These two curves, which estimate the age of the larger limpets, both suggest that, at eeksea station, the mature size of about 3·5 to 4·0 cm. is not reached until the 5th wing season.

Further evidence of the growth rate of the larger individuals was obtained in 1954. February, a collection of chains, some of which were attached to oyster shells, was dged from Section 8 of the river Roach. All the individuals were measured without turbing the chains. Chains in which the individuals were not conveniently accessible measuring were discarded. Each chain was tagged with a numbered plastic button ached by a stainless steel wire passing through a small hole drilled in the diaphragm of bottom dead slipper limpet in the case of free chains or through the oyster shell in the e of attached chains; thus each slipper limpet could be traced by reference to the chain nber and its position in the chain.

Sixty-six marked chains were returned to the river. To assist in finding the chains an a frame 1 m. square was laid on the bottom and the chains were distributed within it by ing, using aqualung equipment. The frame lay nearly flush with the bottom, and the per limpets were lying in their natural habitat, at a depth of about 3 m. at low water spring tides.

The frame was visited by the diver eight months later, and 8 chains of slipper limpets e recovered. The other chains were missing and it is uncertain whether they were placed by commercial fishing operations, or were rolled out by the tide. Nineteen chains e recovered during the following week by dredging in the vicinity of the frame.

There were 111 slipper limpets in the 27 chains recovered and the increment in shell gth of each of the slipper limpets for the growing season of 1954 is compared with the gth at the beginning of the growing season in Fig. 12. The results are in agreement h the estimates made of the growth rate of the larger animals in Fig. 10. It is clear that wth is slow at lengths over about 35 mm. Four limpets were attached to flat shells but ir growth rate was similar to that of individuals of the same size which were in chains.

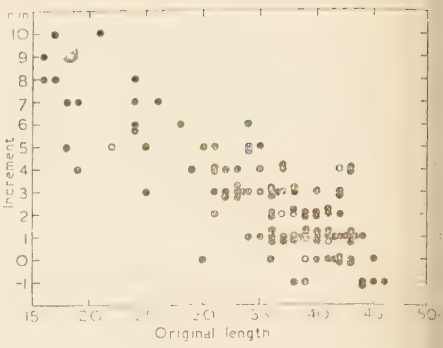


Fig. 12. *The increment in length of* 111 *specimens of* C. fornicata *from February* 26 *to October* 31, 1954. *The slipper limpets were laid in Section* 8 *of the river Roach at a depth of* 3 *m. below L.W.S.T. The open circles indicate individuals which were attached to oyster shells.*

Thus the slow growth rate of the larger individuals was due to factors other than t restricted size of the substrate to which they were attached.

From Fig. 12 it may be estimated that an individual measuring 15 mm. at the beginni of the growing season will reach a length of 24 mm. by the end of that season. By the e of the second season its length will be 30 mm., by the end of the third, 34 mm., by the e of the fourth 37 mm., and by the end of the fifth about 39 mm. Observations report previously in this paper show that a length of 15 mm. is not reached until the end of t second growing season. An individual of 4 cm. is therefore about 7 years old which is agreement with the estimates provided by Fig. 10.

(*c*) *Size of Females*

The effect of the sex-change on growth-rate is uncertain, although Coe (1942) suggested that there is a temporary increase.

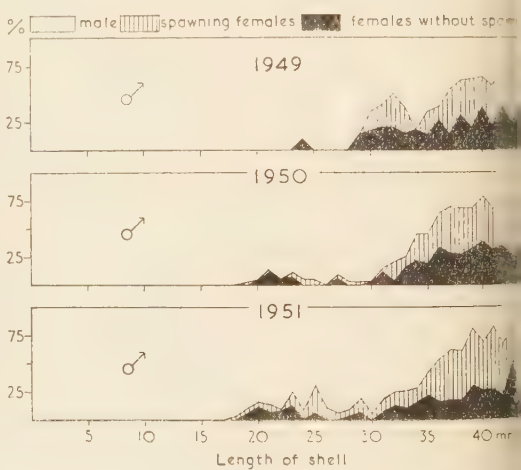
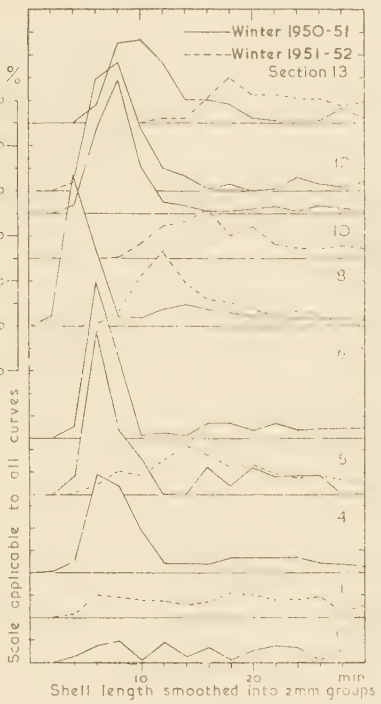


Fig. 13. *The proportion of males and females in each size-group at Creeksea in three consecutive breeding seasons. The females are divided into those which were covering spawn and those which were diagnosed as females on morphological grounds.*

The samples taken from Creeksea during the summers of 1949, 1950 and 1951 ha been combined for each summer and the slipper limpets in each size-group separat according to whether they were male, female without spawn, or female covering spaw (Fig. 13). The correspondence of the curves of females without spawn with the curves f those individuals which were covering spawn, shows that the diagnosis of the sexu condition of an individual by recording the presence or absence of a large penis w accurate.

The smallest female found was one of 18 mm. and there were few females amo slipper limpets of less than 30 mm. Most breeding females at Creeksea are probably least four years old. There does not seem to be any limit to the size of males but, since t proximal and hence oldest slipper limpets of the chains in these samples were near invariably female, most slipper limpets must eventually achieve the female state.



.14. *Showing the size of the* 1950 *group in ious sections of the estuary of the Crouch in the ters of* 1950-51 *and* 1951-52. *The abundance of h size-group is plotted as a percentage of the total ulation. The same vertical scale is applicable to all graphs.*

GROWTH IN OTHER PARTS OF THE RIVER CROUCH

The 1950 spatfall of slipper limpets was the heaviest in 7 years at Creeksea. The les taken from throughout the estuary in the following winter (Fig. 14) show that in preceding summer a very distinct spatfall occurred almost everywhere. The Creeksea les show that the spatfall occurred in the last half of June and, since all the curves f the same general shape, it is probable that the spatfall occurred throughout the ary at about the same time. The conditions during June must have been unusually good he growth and metamorphosis of the larvae.

f the spatfall did occur throughout the estuary at about the same time, an examination ie position of the peak size of the O-group slipper limpets in the following winter give some indication of the relative merits of various parts of the Crouch estuary for growth of juvenile *C. fornicata*. The position of this mode (Fig. 14) is at a low figure of t 4 mm. at Creeksea and gradually increases to about 10 mm. towards both the head rs and the mouth of the estuary. The middle reach of the estuary was apparently less ble for the growth of the juveniles than either end. Unfortunately, fewer samples are able for the winter of 1951/52, but those which are available make it clear that the group was still doing better in the upper and lower reaches than in the middle of the ary.

GROWTH IN THE ENGLISH CHANNEL

. fornicata is now widespread in the English Channel and information on its growth- in this off-shore environment is of interest in comparison with that recorded from ered Essex creeks. Orton and Rogers (1950) record the shell length of a number of mens which were obtained from the shells of escallops, *Pecten maximus*, which had caught in Lyme Bay in depths varying from 8 to 35 fathoms. These data can be ped (Table 9) into those from limpets which were caught in the winter of 1947-1948 hose caught in the spring and summer of 1948; they are shown in Fig. 15 with the size iencies of two samples obtained by my colleague Mr. R. H. Baird. These two latter les, collected in the spring of 1953 and 1954, were also from the shells of escallops but caught farther east in the Channel.

Table 9: *Age related to length in a sample of* 69 Crepidula *from Lyme Bay. Tabulated from Orton and Rogers* (1950)

Length mm.	Years					
	1½	2½	3½	4½	5½	6½
1 – 10	9	–	–	–	–	–
11 – 20	7	1	–	–	–	–
21 – 30	–	9	3	–	–	–
31 – 40	–	6	21	2	–	1
41 – 50	–	–	7	1	2	–

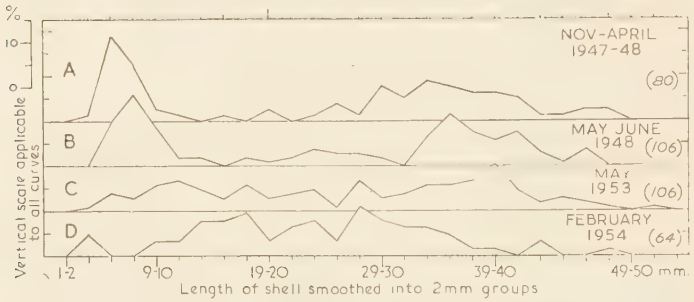


Fig. 15. *The percentage size-composition of three populations of* C. fornicata *in the English Channel. The same vertical scale is applicable to all graphs. The numbers in the samples are shown in brackets.*

(A) and (B) Population on escallop shells in Lyme Bay (abstracted from Orton and Rogers, 1950b).
(C) Population on escallop shells 16-20 miles south of Newhaven.
(D) Population on escallop shells 10 miles south of Worthing.

In all these Channel samples, the size range of *C. fornicata* in their first winter an spring is 4 to 14 mm. which is of the same order as in Essex. Orton and Rogers (195 postulated a peak size of 5 mm. at an age of one summer in Lyme Bay, although their da suggest a somewhat higher figure. Many of these individuals were either solitary c members of very small chains and annual rings could be distinguished in many individua Orton and Rogers' information on the probable age of the many individuals caught in t period 19.11.47 to 21.6.48 is tabulated in Table 9. These data suggest a growth-rate rath faster than that found by the author for the Essex rivers; the mature size of 4·0 cm. reached in Lyme Bay in the 4th or 5th summer. It should be remembered, however, tha these are individuals with a comparatively flat shell and it has been shown previously tha such specimens may grow more rapidly in length, although not in weight, than individua in chains. The heights quoted by Orton and Rogers are typical of limpets growing on flat surface.

4. MAXIMUM SIZE

It has been shown previously (p. 20) that about one slipper limpet is added to a chai each year and yet in many chains several adjacent mature females of similar size are foun Individuals tend to grow to the mature size for their particular habitat, after which on slow growth occurs, and individuals of different ages, but similar size, accumulate at t bottom of the chains. Since nearly all slipper limpets eventually change to the fema

ndition the comparison of the size of the larger females will give an index of the quality a particular habitat for their growth. A satisfactory measure of the size attained by the nales is given by the percentage of females which exceed a given size. This is more formative than the maximum size found at a particular station and the mean size is satisfactory as the size frequencies of the females are not normally distributed. A useful ıtistic is the proportion of the females which exceed 45 mm. In the samples measured ɔm various parts of the river Crouch, few slipper limpets exceeded this size and in ctions 3-13 inclusive no sample contained significantly more large individuals than the st. Single samples measured from each of Sections 0 and 2 contained significantly = ·01) more large females than those from the rest of the estuary.

Growing conditions for slipper limpets in the river Roach are evidently generally better an in the Crouch as the females in samples from Sections 7, 8 and 9 were significantly ger than most of those from the Crouch, although a sample measured from Section 6 ıs not.

One sample from Poole Harbour (South Deep) showed that growing conditions were cellent as 60 per cent of the females were larger than 44 mm. and one measured 66 mm. the largest individual found by the author.

3. BREEDING AND SPATFALL IN THE RIVER CROUCH

ıble 10: *The numbers of juvenile and adult slipper limpets from one sq. metre in various places*

Station	Distance from low water mark m.	Depth at low water m.	No. of chains in 1 sq. m.		No. of slipper limpets in 1 sq. m.		No. of 0-group not attached to chains
			Free	Attached	0-group	Older than 0-group	
River	100	8	17	2	12	67	1
Blackwater	150	7	66	1	70	374	2
Section 3	200	7	4	0	4	25	1
	250	7·5	96	3	194	594	1
River	25	4·5	5	0	0	10	0
Roach	50	4	20	25	70	104	17
Section 8	100	7	18	1	17	103	0
	150	4·7	9	0	0	26	0
River	50	7	5	0	5	17	0
Roach	75	8	29	0	30	132	5
Section 7	125	10	95	15	220	441	16

series of grab samples was taken to study the distribution of the 0-group in the winter 1949-50. At two places in the river Roach and at one place in the river Blackwater a line stations was marked across the river. 10 hauls were made with a 0·1 sq. metre Petersen ab giving a sample of 1 sq. metre from each station. The clusters of limpets were picked t and all pieces of shell and stone were searched for small individuals. All the limpets ere measured and the number of 0-group estimated from size-frequency diagrams able 10). A few were attached as epifauna to dead shells of oysters, cockles, and limpets, ıt the great majority were attached to living chains of slipper limpets. By this time, the veniles were moving into favourable positions on the chains.

On each of the three lines, the stations were close together. The maximum distance tween stations in the river Blackwater series was 150 metres and in the two series from e river Roach 125 and 75 metres. It is probable therefore that each station of a series ıs equally exposed to a spatfall, but in fact the number of 0-group limpets per square etre was closely related to the number of older limpets. As the abundance of the spatfall ıs of the same order in each of the three series of stations, the results have been combined

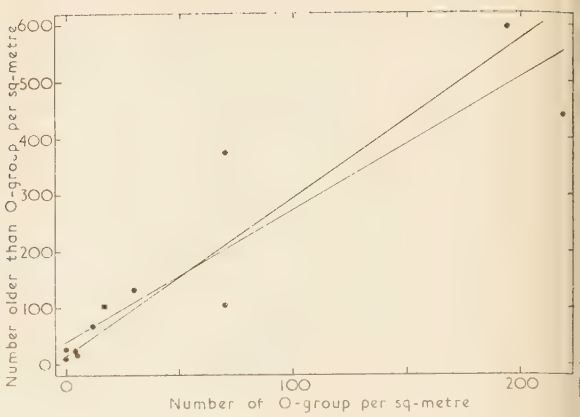


Fig. 16. *The relation between the abundance of* 0*-group* C. fornicata *and the abundance of adults* (*see Table* 8).

(Fig. 16). Statistically the correlation between the abundance of 0-group slipper limpets and older limpets is highly significant ($r = 0{\cdot}9158$, $P > {\cdot}001$). The two regression lines have been drawn and show clearly that, on these grounds, the proportion of juveniles was directly correlated with the abundance of adults.

These observations were made 6 to 9 months after the larvae had metamorphosed and, since the juveniles are mobile, it cannot be assumed that they actually settled in the proportions found on each of the square metres sampled. It is possible that in the first year active movement may take place until the juveniles find a cluster of slipper limpets with which they may become associated. Thus dense patches of slipper limpets on the bottom would have the density of juveniles increased by immigration, whereas patches with few adults would lose many juveniles. If this were the case, however, the clusters in the low density areas would be expected to carry a higher proportion of juveniles than those in the high density areas, although the actual numbers of juveniles per unit area would be low. As this is not the case, it seems that the juveniles must have metamorphosed close to, or even on, the clusters of adults.

Knight-Jones (1952) observed the weekly spatfall of *Ostrea edulis* in the rivers Crouch and Roach by exposing test slates in various parts of the estuaries. A note was also kept of other organisms found on the slates and it is remarkable how few post-larval *C. fornicata* were seen. In 1948 a total of 6 was counted on all the slates in the whole summer, compared with 314 oyster spat, whilst in 1949 the totals were respectively 2 and 108. From the abundance of *Crepidula* compared with oysters, in the estuaries, and the number of juveniles which are found subsequently on the bottom, a greater spatfall would have been expected on the test slates. It is suggested that the paucity of the settlement on the slates is due to the larvae being very gregarious so that most of the settlement takes place on the chains.

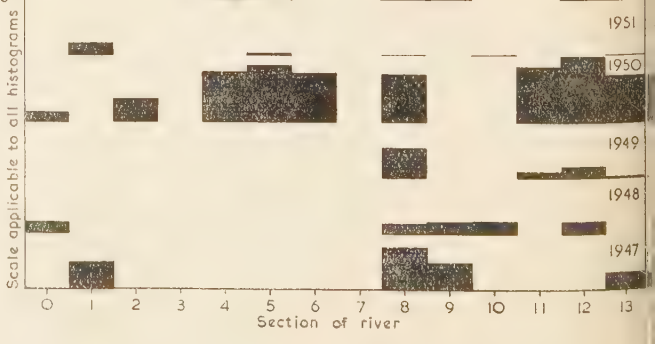


Fig. 17. *The proportion of the* C. fornicata *population which was represented by the* 0*-group in various sections of the river Crouch for* 7 *successive winters. Where more than one sample was measured from a section, the samples have been combined.* (*Blanks indicate absence of observations*).

In the winter months, the majority of the 0-group are attached to chains, although the ethod by which this state was brought about is uncertain. By measuring samples of chains limpets in the winter an estimate can be made of the recruitment to the stock. In Fig. 17 ıe estimate of the spatfall in the sections of the Crouch estuary from which samples are ailable for each of the winters from 1947-48 to 1953-54 has been plotted. In those cases here more than one sample was measured in a section, the mean of the percentage of the veniles in the samples has been plotted. The average percentage of 0-group slipper mpets in individual sections varied in the 7-year period from nil to 73·9 per cent and the erage for the whole estuary varied from 3·4 per cent to 50·4 per cent. The average rcentage abundance of 0-group slipper limpets for 7 consecutive winters was 19·0 per nt; i.e. on the average, each winter the 0-group comprised about one-fifth of the stock.

In 1948, 1950 and 1951, the spatfall was at about the same level of intensity throughout ıe Crouch. In 1947, 1949, 1952 and 1953, the spatfall was lighter high up the estuary ıan in the middle and lower reaches. Parts of the lower reaches of the estuary received a arkedly higher spatfall than the rest. The causes of such discontinuous spatfalls are not ully known but many hydrographical and meteorological factors play a part in determining stribution.

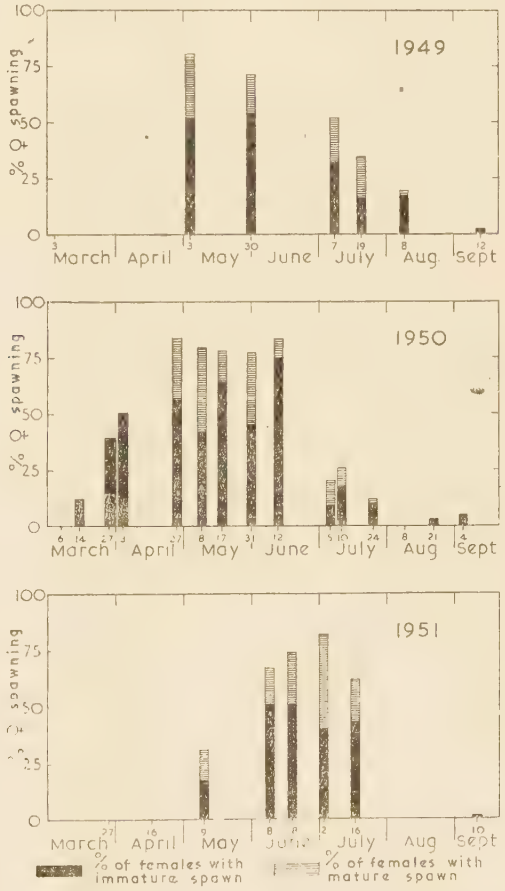


Fig. 18. *The proportion of females which were covering newly laid spawn, or covering mature spawn (late veliger stage), in the routine samples from Creeksea in* 1949, 1950 *and* 1951.

The spawning of *Crepidula* begins when the water temperature has risen to about 10° C. hipperfield, 1951); usually this occurs in April in the river Crouch. In 1949, many of e spawned females at Creeksea were covering late veliger larvae in early May (Fig. 18) ıd spat appeared in numbers between July 7 and July 19. In 1950, larvae were liberated the end of April and the beginning of May, and spat appeared on the clusters between ıne 12 and July 5, slightly earlier than in 1949. In 1951, spawning was markedly later.

This was probably correlated with the cooler spring of that year. The mean May wate temperature was 3° lower than that of 1950 and 2° lower than that of 1949.

The abundance and growth of oyster larvae (*Ostrea edulis*) have been observed in th river Crouch during each summer of the period 1948-1953 and it is of interest to compar the success or failure of oyster larvae and slipper limpet spat in each of these years. Detail

Table 11: *River Crouch. Mean spatfall of slipper limpets, expressed as the percentage of the population during the following winter, related to the mean number of recentl liberated and mature oyster larvae occurring during June, July and August*, 1948-1953.

	1948	1949	1950	1951	1952	1953
Mean number of oyster larvae (<·22 mm.) per 100 l.	18·7	15·9	74·8	25·9	84·3	36·8
Mean number of eyed oyster larvae per 100 l.	0·79	0·64	6·00	0·00	0·33	0·30
Eyed larvae expressed as % of freshly liberated oyster larvae	4·2	4·0	8·1	0·0	0·4	0·8
Slipper limpet spatfall as % of population	12·9	14·6	50·4	3·4	9·4	10·2

of the growth and settlement of oyster larvae in the years 1947 to 1949 have already bee published, (Knight-Jones, 1952) and for the use of the data for the years 1950-1953 I a indebted to my colleague Mr. G. D. Waugh.

The method of pump sampling used to determine the abundance of oyster larvae h been described by Knight-Jones (1952). Table 11 gives the mean numbers of recenti liberated larvae, which measure less than 0·22 mm., and of mature larvae in the routin 100 l. samples taken each year in the three months of June, July and August. Norm three samples, spaced at intervals along the Crouch estuary, were taken twice weekly the time of low water.

A general index of survival and growth of oyster larvae is obtained by expressing th mean number of mature larvae as a percentage of the numbers of recently liberated larva In a good year, a larger proportion of larvae would be expected to grow to maturity th in a bad year. From a study of the figures in Table 11 it seems that, in the river Crou this index of growth of oyster larvae is positively correlated with the abundance of youn slipper limpets; a good year for slipper limpet spat is a good year for the growth of oyst larvae. Knight-Jones (1952) has concluded that food supply is probably the princip limiting factor in the growth of oyster larvae in the river Crouch and it seems likely that th planktonic larvae of *C. fornicata* require organisms similar to those known to promote goo growth and settlement of oysters (Bruce, Knight and Parke, 1940).

Part IV. Distribution of *Crepidula fornicata* and the other principal epi-benthic invertebrates of the rivers Crouch & Roac

1. GENERAL FEATURES OF THE ESTUARIES

The courses of the two rivers lie in the Eocene London Clay of S.E. Essex. The rive are short and the average rainfall in the catchment area is low (ca 450 mm. per annum

g. 19. *The estuaries of the Crouch and Roach, the sections into which they are divided, and the rounding topography. The land over 30·5 m.* (100 *ft.*) *above sea level is stippled. The 5 fathom* (9·1 *m*) *depth contour is shown as a dotted line.*

e general topography is shown in Fig. 19, the land 30·5 m. (100 ft.) above ordnance .um being picked out by dark stippling (extreme high water at Burnham-on-Crouch is m. above ordnance datum). Some of the large areas of sand banks lying outside the uth of the river and uncovered at low tide are also shown. These sand banks have a .siderable effect on the temperature of the incoming tide.

For the purpose of this study the estuaries were divided into sections of 1,600 metres e mile), numbered serially from the mouth of the river Crouch. In the upper reaches, zone of most rapid change, the sections are further sub-divided.

The river Crouch has a total length of 45 kilometres of which 29 are tidal. The stream s at about 30 m. above sea level and serves a catchment area of about 228 square ometres, discharging into a long narrow estuary which gradually widens to 1·8 kilometres he mouth, with a maximum depth of 9 metres at low water.

The river Roach flows into the Crouch 6·4 kilometres above its mouth; it has a total gth of 21 kilometres of which only 6·4 are non-tidal. Both estuaries are bordered by sea ls, as the surrounding countryside is two or three metres below high water mark.

The maximum tidal range at Burnham is about 5·5 metres, decreasing to about metres at Battlesbridge.

The maximum depth encountered in each section of the rivers Crouch and Roach ing this survey is shown in Fig. 20. Representative cross sections of various parts of the uaries are shown in Fig. 21. Mud and clay are the predominant features of the shores l bottom. No rock occurs, contours are gradual and it is possible to dredge everywhere.

In the development of the climax community of the lower parts of the estuaries the

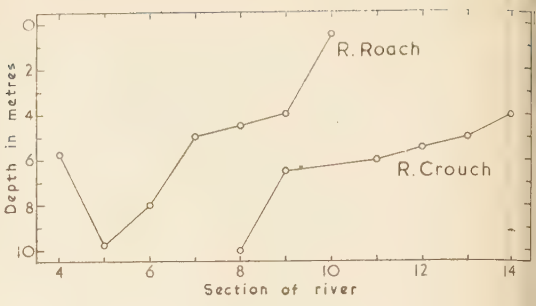


Fig. 20. *The maximum depths recorded in this survey in various sections of the estuaries of the Crouch and Roach.*

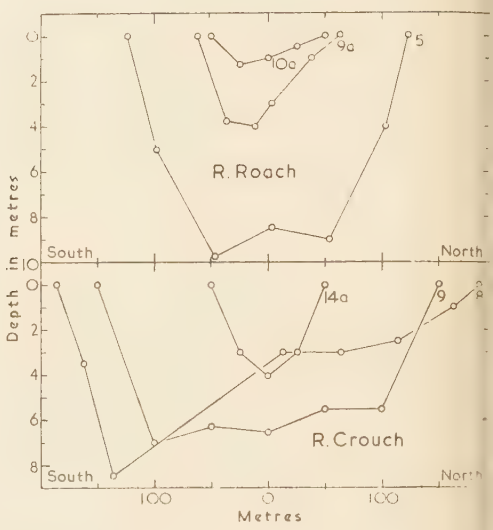


Fig. 21. *Representative cross-sections of various parts of the estuaries of the Crouch and Roach.*

mud may become overlaid with dead shells, principally of the genera *Crepidula*, *Macoma*, *Mya*, *Ostrea* and *Paphia*. This climax is only reached in some parts: in others the bottom may be nearly pure mud, without stones or shells, or the mud may be densely covered

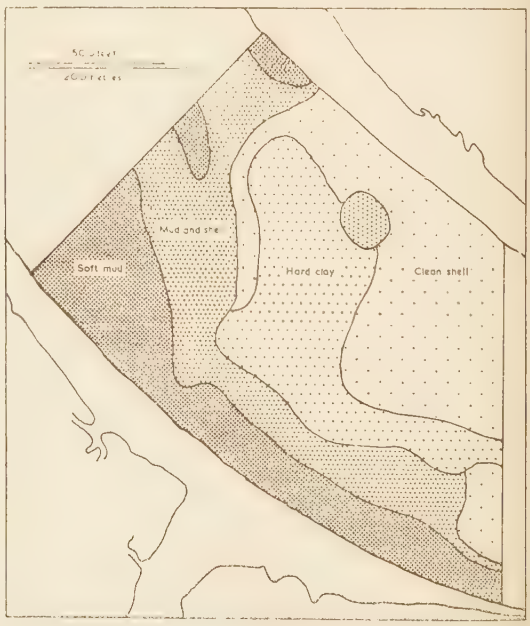


Fig. 22. *The nature of the bottom in a small area of the Crouch estuary at Creeksea.*

epidula. In the latter case, the mud may be secondary, being largely built up from the ces and pseudo-faeces of *Crepidula*. Locally a very firm compact clay occurs which is ually riddled with the burrows of boring lamellibranchs, especially *Petricola pholadiformis*. similar hard clay and associated fauna is reported from the south side of the Thames uary (Newell, 1954). Fig. 22 shows the very varied nature of the bottom which may be und in a small area (part of section 8 of the river Crouch). No significant difference was und here in the numbers of epi-benthic forms on the different types of bottom.

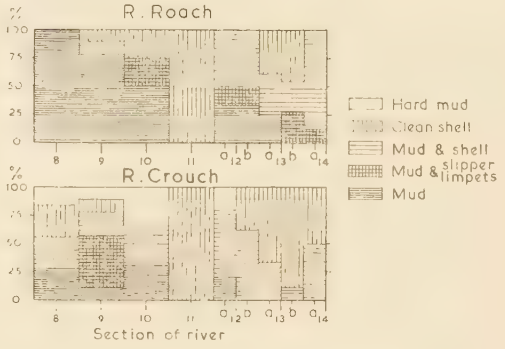


Fig. 23. *The proportion of stations located on each of the five main types of bottom deposit in the various sections surveyed in the rivers Crouch and Roach.*

In the survey, the nature of the bottom has been broadly classified into 5 groups: an shell, mixed mud and shell, mud, hard clay, and mud with slipper limpets. The portion of stations on each of these five types in each section examined in the rivers ouch and Roach is indicated diagrammatically in Fig. 23. In both estuaries mud is re prevalent in the lower reaches.

2. HYDROGRAPHY AND WEATHER

ater temperature (Fig. 24) was continuously recorded at Paglesham in the river Roach ction 8) by a thermograph mounted on a pontoon moored in mid-stream in 5 metres water, the bulb being 2 metres below the surface. The water temperature was also orded in section 12 of the river Crouch for the year June 1951-May 1952 (Fig. 24).

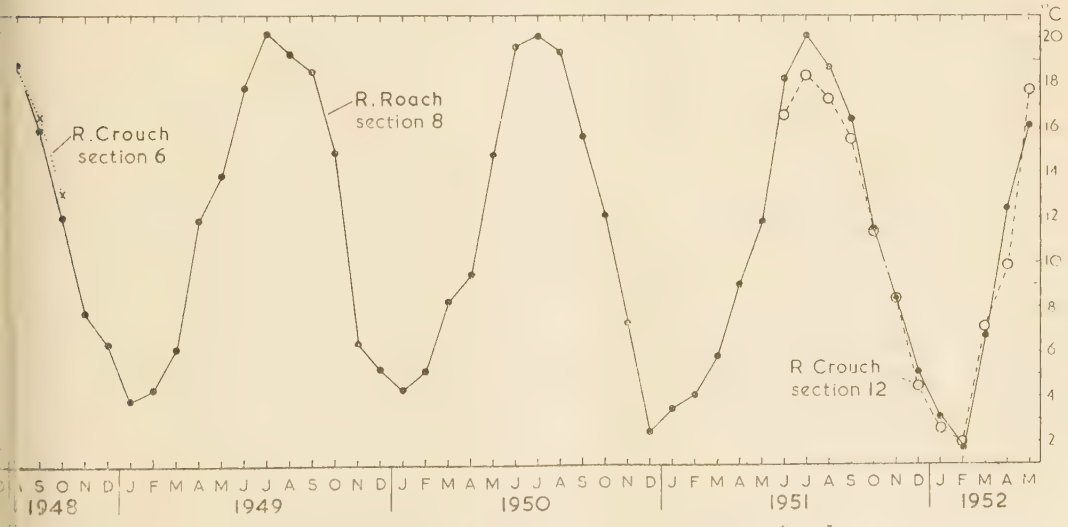


Fig. 24. *The monthly average water temperature in the estuaries of the Roach* (*Sect.* 8) *and the Crouch* (*Sects.* 6 *and* 12).

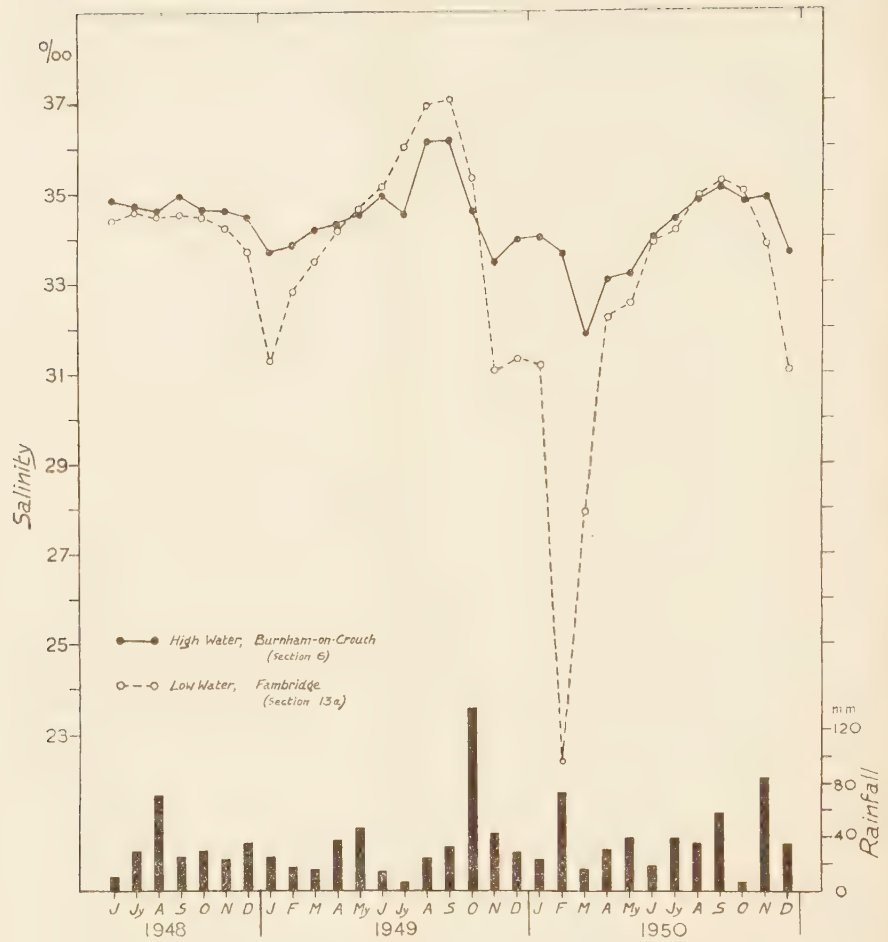


Fig. 25. *The monthly average surface salinity in the estuary of the Crouch.* (*Sect.* 6 *and* 13*a*).

Surface salinity samples were taken occasionally at Burnham (Section 6) at high wat and at Fambridge (Section 13a) at low water. The monthly averages of these records a given in Fig. 25. As river discharge is low, the salinity in the upper reaches rises above th of the outside sea water in hot summers. Very high values were recorded during 194 36·47‰ at high water at Burnham-on-Crouch on August 16 and 37·47‰ at low water Fambridge on September 7.

Table 12 gives a comparative picture of the surface salinity in different parts of th Crouch and Roach from samples taken simultaneously in the two rivers. In both estuari there is generally little tidal fluctuation of salinity where the depth of water at low tid exceeds 5 metres.

Knight-Jones (1952) gives an account of some experiments with drift indicators whic showed that on moderate tides planktonic larvae could be transported about 8 kilometr in 6 hours. Clearly, larvae liberated anywhere in either estuary have ample opportunity be widely dispersed during the planktonic stage.

3. METHOD

The primary purpose of this part of the investigation was to obtain a picture of th distribution of *C. fornicata*. *Crepidula* is normally sub-littoral but where considerab numbers were exposed at extreme low water the distribution of clusters was seen to b

Table 12: *Low water surface salinities recorded from the river Crouch and river Roach*

Place	Section	1947			1948					1949										
		Jul. 13	Dec. 22	Dec. 23	Jan. 15	Jan. 30	Feb. 16	Feb. 23	May 21	Jan. 5	Jan. 11	Feb. 8	Feb. 17	Feb. 18	May 17	Jul. 23	Oct. 25	Dec. 12	Dec. 13	Dec. 16
River Crouch Battlesbridge	18a	–	–	–	–	–	–	–	–	0·53	–	–	–	–	–	–	3·40	–	–	–
Hullbridge	16a	–	–		19·70	12·81	19·96	27·31	–	2·50	16·68	26·72	24·50	–	–	–	14·57	–	–	
Brandy Hole	14b	–	–	–	–	–	–		–	19·43	–	–	31·00	30·50	–	–	–	–	–	–
Clements Green Creek	14a	–	–	–	–	–	–	–	–	–	–	–	–	32·10	–	–	–	–	–	–
Fambridge	13a	–	–	33·36	31·90	31·97	31·57	31·87	34·31	29·93	31·23	32·87	32·77	–	34·68	35·77	33·88	32·17	–	–
Bridgemarsh	10	–	–	–	–	–	–	–	–	32·48	–	–	–	–	–	–	–	–	–	–
Creeksea	8	–	–	–	–	–	–	–	–	33·50	–	–	–	–	–	–	–	–	–	–
Burnham	6	35·10	33·53	33·91	32·95	32·85	32·66	32·87	–	–	–	33·33	33·53	–	34·80	35·67	33·12	–	–	–
River Roach Barton Hall Creek	10b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25·89	–	29·91	27·90
Common Shore	9a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	31·10	–	–	–
Paglesham	8	34·90	33·51	–	32·23	30·81	32·10	31·93	34·43	–	–	–	–	–	–	–	31·91	–	–	–

patchy; they had accumulated into shallow banks, one or two metres in width, an approximately at right angles to the current. The patchiness was found to extend belo low water mark as shown by the following experiment made in Section 5 of the rive Crouch. An area 50 metres square, varying in depth from 2 to 4 metres at low water spring tides, was marked out by 4 buoys. In this square 5 samples were taken at each 10 stations with a 0·1 sq. metre Petersen grab. The numbers of *C. fornicata* chains obtaine at each station varied very considerably; the two highest concentrations—53 and 4 clusters—were found only 20 metres from the two lowest (3 and 2 clusters). Thu considerable differences in population density may occur in a very small area and ther would be difficulty in surveying adequately a large area with a grab. It was therefore decide to employ a technique which would permit of the sampling of larger areas of botton For this purpose an oyster dredge seemed the most suitable instrument available. The preser survey thus supplements and extends that of Mistakidis (1951) who used the gra intensively on two grounds.

To estimate the efficiency of the dredge used, ten 50 metre hauls were made at interva over the same ground as had been examined in the grab experiment detailed above. Th densities of *C. fornicata* recorded by the grab on the various stations differed so widel that it is not useful to compare each dredge haul with the probable limpet population ov which it passed. The mean of the 50 grab samples from the whole area was 22·5 cluste per 0·5 sq. metre, equivalent to 1,372 clusters per 30·5 sq. metres, the approximate are covered by the dredge in each haul (see below). The mean number of clusters taken p dredge haul (10 hauls) was 228, giving for slipper limpets an approximate efficien compared with the grab, of 16 per cent. Although the efficiency of the hand dredge is th rather low, yet, when the results from the whole survey are examined, they give a intelligible pattern for the distribution of the larger epi-fauna; moreover, the upper p of the Crouch estuary has been surveyed in three consecutive years and each year a sim distribution pattern has been recorded. It was therefore concluded that the hand dre was sufficiently reliable for our purpose.

The dredge used had a scythe of 0·61 metres. The belly of the bag was of galvanise iron rings, 2·5 cm. in diameter, and the top a net of similar mesh. The dredge was tow from a launch, with the flow of the tide, and as slowly as practicable. The mean dura of thirty dredge hauls was 49·6 secs. The length of the tow-rope used was three to fo times the depth of the water; this allowed the dredge to dig fairly well into the bott The length of tow at each station was 50 metres, which on a soft bottom just sufficed to the bag. The area covered by one haul was approximately 50 × 0·61 metres (width scythe) or 30·5 sq. metres.

Lines of stations were worked at intervals of approximately 400 metres along courses of both the rivers Crouch and Roach. Each line, or set of stations, comprised series spaced at 50 metre intervals across the river between low water marks. Sometim two, but usually three or more hauls, were made at each station and all results are expresse as the average of all the 50 metre dredge hauls taken at a given station.

The position of the stations in the river and relative to the river bank was determin in the following manner. The end of a length of line was anchored to the edge of the sa marsh or to the bottom of the sea wall, the position of both being marked on the 1 : 103 Ordnance survey map. The line, marked every 25 metres, was wound on a reel on boa and was run out as the boat headed for the opposite shore. Small buoys, attached to block were dropped every 50 metres, starting at the first mark after passing low water mar It was impracticable to handle more than 300 metres of line so that some of the wid reaches of the estuary had to be dealt with in two stages, working from opposite shores.

Two methods were used to standardise the length of the haul at 50 metres. At fir 4 posts were erected at the corners of a rectangle on the salt marsh lining the bank so as mark two parallel sight lines, 50 metres apart, running across the river. The boat work with the tide, its distance from the bank being determined by the appropriate buoy, and the first two posts came into line the dredge was then shot and towed until the second tw posts came into line. In the second method, which soon superseded the first, a 50 met line, with a buoyed and vaned float attached to one end, was fixed to the marking buo

e float was caught by the tide and streamed out the 50 metre line taut from the marking y. The dredge haul was then made as close alongside the line as was practicable. The a obtained from all the dredge hauls in each section have been grouped together to give ean value per dredge haul for each species in that section.

The detailed survey covers Sections 8 to 15 in the river Crouch and from the mouth ction 4) to Section 10A of the river Roach.

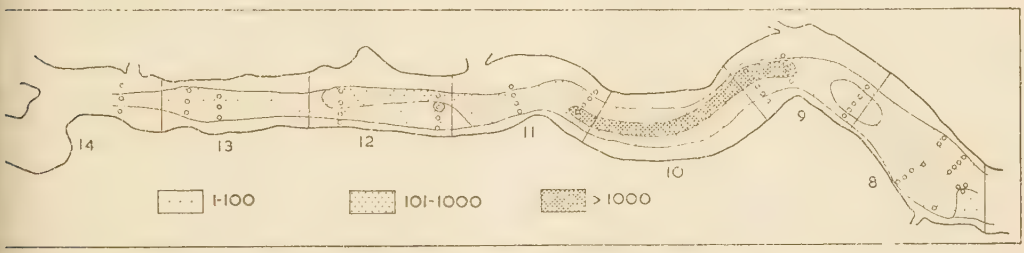
4. RESULTS OF THE SURVEY

(a) Distribution of Crepidula fornicata

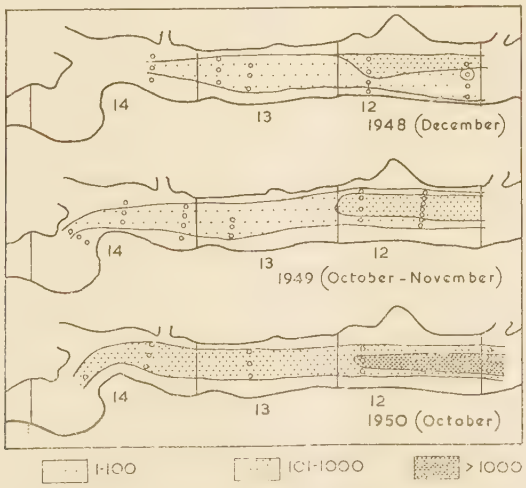
e mean number of *Crepidula* in a 50 metre dredge haul at each station has been plotted a chart. Contoured diagrams prepared from these charts are shown in Figs. 26, 27 and 28. e mean numbers caught in the various sections of the river are summarised in Figs. 29, and 31.

The survey of Sections 8 to 14 of the river Crouch (Fig. 26) was made from October December 1948, except for 5 stations in Section 8 which were worked in February 1949. that time *Crepidula* was most abundant off Bridgemarsh Island where at two of the ions worked more than three thousand limpets were caught per dredge haul.

The winter of 1946-47 was unusually severe; there was an 'exceptional wintry spell ompanied by persistent easterly winds and considerable snowfall from about January 23 il mid-March'. In the second half of March 'thawing snow accompanied by frequent a caused unprecedented floods over large areas of England and Wales'. (Monthly



.26. *The abundance of* C. fornicata *in Sections* 8-14 *of the river Crouch in the winter of* 1948-49. *The open circles represent dredging stations.*



.27. *The abundance of* C. fornicata *in the upper Crouch in three consecutive winters, showing repopulation following the severe frost of* 1947.

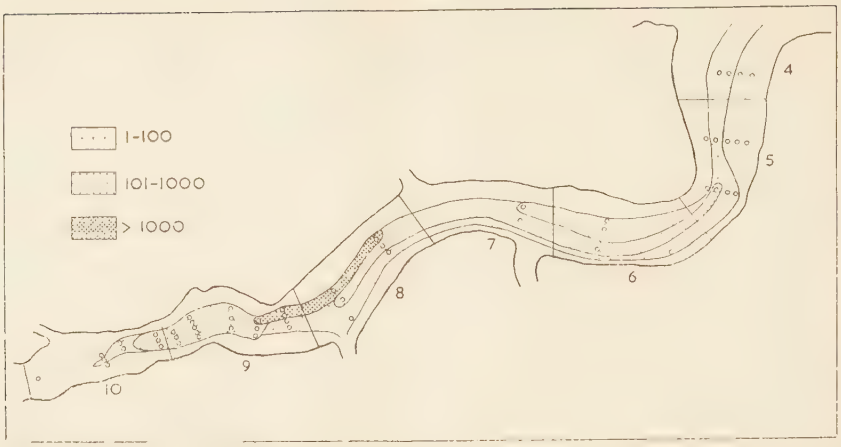


Fig. 28. *The abundance of* C. fornicata *in Sections* 4-10 *of the estuary of the river Roach in th winter of* 1949-50. *The open circles represent the position of dredging stations.*

Weather Report of the Meteorological Office, Summary for year 1947). Records are no available from the rivers for that period, but it is clear that very cold conditions persiste for some time, and, when the thaw came, there was a considerable reduction in the salinity Ice was prevalent in the estuaries of the Crouch and Roach for several weeks. This sever weather resulted in the extermination of *C. fornicata* from Sections 13 and 14 of the riv Crouch, and, judging by the number of dead shells found in this survey, there wa considerable mortality in Section 12.

Sections 12 to 14 of the river Crouch were surveyed again in November 1949 and October 1950 to observe re-colonisation. In Fig. 27 contoured diagrams for each of t three surveys of the upper part of the river Crouch are shown. It is clear that, except af exceptional weather conditions, this part of the river normally supports a considera population of *C. fornicata*. A similar recolonisation by other species of epi-benthic inver brates was also found (Fig. 30).

The survival of *C. fornicata* in wire-covered cages in Section 14b of the river Crouc and in Section 8 of the river Roach was observed during the winter of 1949-195 On November 25, 1949, slipper limpets were caught off Bridgemarsh Island (Section river Crouch) and placed in the cages. One cage hung below a pontoon in the river Roa while the other lay on the bottom in Brandy Hole (Section 14b, river Crouch). On March 2 1950, the two cages were recovered and the dead and live individuals counted (Table 1 Some mud had accumulated in the cage in Brandy Hole and this may account for part of t mortality (15·7 per cent) which was in excess of that in the tray at Paglesham (5·9 per cent This experiment confirms the deduction made from the survey results that many individua will survive a normal winter in the upper Crouch estuary.

Table 13: *The numbers of live and dead slipper limpets after exposure in trays in the upper par of the Crouch estuary and the middle part of the Roach estuary. The trays were in positio from* 25.11.49 *until* 24.3.50

Station	Free clusters		Attached clusters		Total		% Mortality
	No. of slipper limpets	Average size of clusters	No. of slipper limpets	Average size of clusters	Number alive	Number dead	
Brandy Hole (Sect. 14b, river Crouch)	1,527	5·49	324	4·50	1,851	344	15·7
Paglesham (Sect. 8, river Roach)	2,083	7·43	315	7·15	2,398	145	5·9

Sections 4 to 10 of the river Roach (the complete range of *C. fornicata*) were surveyed he period December 1949 to February 1950. Few limpets (Figs. 28 and 31) were found he muddy lower reaches, probably because of the lack of suitable settling surfaces for larvae. They were present in large numbers in Sections 8 and 9 but did not occur above tion 10a.

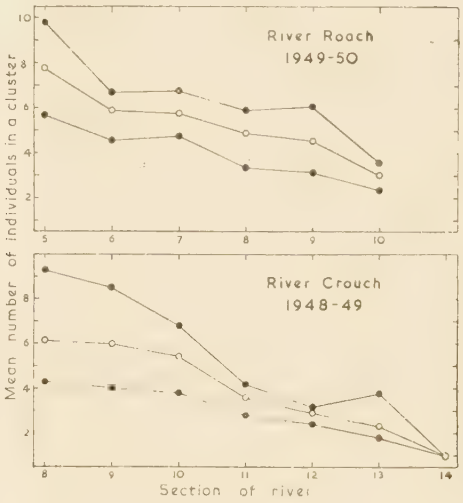


Fig.29. *The average number of* C. fornicata *in free clusters in each section of the river. The highest and lowest values found in each section are also shown.*

In areas liable to unsuitable conditions, e.g. extreme cold or an influx of fresh water, clusters of slipper limpets will not grow so large as in areas where the conditions are e uniformly satisfactory. The average number of slipper limpets in free clusters has n calculated for each station in the 1948 river Crouch survey and in the river Roach ey and from these data the mean size in a section has been calculated. Fig. 29 shows the est and smallest mean cluster size recorded in each section and the mean for the section. oth estuaries, the size of the free clusters declines steadily towards the head waters. he river Crouch the average cluster size decreases most rapidly above Section 10, while he river Roach the cluster size decreases sharply in the second and last Sections nd 10). In both estuaries, proximity to the sea favours the formation of larger clusters. No evidence was found to suggest that the cluster size at a station was related to the ulation; a large population did not necessarily have either larger or smaller clusters adjacent populations which were less dense.

t is of interest to consider the range of environments in which *C. fornicata* thrives. re are references to its abundance and habitat in the vicinity of the Woods Hole ratory (Massachusetts), but the writer has been unable to trace any similar reference ing to the Canadian coast. Verrill (1873), described it as 'very abundant' in Vineyard nd and Buzzards Bay, from low water mark to 12 fathoms, especially on gravelly and y bottoms. Sumner, Osburn and Cole (1913), in a further survey of the same area, d *C. fornicata* to be the second most frequently caught gastropod. It was generally ibuted down to 19 fathoms on all types of bottom. Large numbers were found in yard Sound, where the bottom was of mud and shells. Lee (1944) made a grab survey art of Vineyard Sound and found up to 629 slipper limpets per 0·5 sq. metre. Its nce from areas of bottom where suitable attachment surfaces were not present was d, as in the present survey. Allee (1923a,b) presenting data on the presence or absence *. fornicata* in shore collections made in the vicinity of Woods Hole, records that it was ent near low water mark in a wide variety of habitats.

he salinity in the Vineyard Sound-Buzzards Bay area varies from 30 to 32‰ and the y temperature range is from — 1° to 24°C. It is clear that *C. fornicata* thrives in this and the maximum density in favourable habitats (Lee, 1944), is very similar to that d in the Crouch and Roach (Mistakidis, 1951).

Dexter (1944, 1947) worked at Cape Ann, about 60 miles north of Woods Hole, beyon Cape Cod. In dredged samples a maximum of 34 per 60 sq. m. and, on the shore, 4 pe 400 sq. in. (ca. 0·16 sq. metre) was recorded.

Slipper limpets occur generally in the sub-tropical conditions of the Gulf of Mexic Hedgepeth (1953) states that '*C. fornicata* is not rare' on the oyster reefs of the Texa coast, but is never sufficiently abundant to be a competitor for food. On these beds, th yearly temperature range is between 17°C. and 30°C. and the salinity varies betwee $30^0/_{00}$ and $36^0/_{00}$ (Port Isabel). Whitten, Rosene and Hedgepeth (1950), studying the faun of training walls on the Texas coast, recorded *C. fornicata* as common on shells inhabite by hermit crabs. This environment was liable to considerable fluctuations of salinity an the temperature varied annually from 12°C. to 31·5°C. Ingle (1951) refers to *C. fornicat* as an important competitor of oyster larvae for settling space in Apalachicola Bay, Florid where the salinity varied from $0·0^0/_{00}$ to $42·5^0/_{00}$ in 18 months and the temperature varie annually from 15°C. to 30°C. *C. fornicata* clearly flourishes in sub-tropical habitats bu probably achieves its greatest size and abundance in the temperate regions.

On the Pacific coast, Hopkins (1937) refers to the great abundance of *C. fornicata* o oyster grounds in Puget Sound. Hydrographical conditions there are more temperate, th annual temperature range is - 2°C. to 28°C. and salinity varies from $23^0/_{00}$ to $28·5^0/_{00}$. It interesting to note that *C. fornicata* flourishes in salinities substantially lower than tha of normal sea water.

(b) Distribution of Other Larger Epi-Benthic Invertebrates

This part of the paper is based on information collected during the survey of th distribution of *C. fornicata*. Certain species can be used as indicators of the suitability any new area for oyster cultivation when the limits of their distribution are known. Th extent to which *Crepidula fornicata* may become a pest if introduced may also be fore by studying the distribution of the species considered below.

Table 14 and Fig. 30 summarise the quantitative distribution of *Solaster pappo Ophiura texturata*, *Buccinum undatam*, *Ostrea edulis*, *Eupagurus bernhardus*, *Macrope rostrata* and *Hyas araneus* in Sections 8 to 15a of the river Crouch in the autumn of 19 The survey of the upper part of the river Crouch was repeated in 1949 and 1950, to st the re-population after the severe conditions of 1946-1947, and the data for these tw surveys is summarised in Tables 15 and 16 and Fig. 31. The results of the survey made the river Roach in the winter of 1949-1950 are presented in Table 17 and Fig. 32. Sc notes are given below on the species recorded quantitatively.

Table 14: *River Crouch* 1948. *Mean numbers of epi-benthic animals per* 50 *metre dredge ha*

Section	8	9	10	11	12a	12b	13a	13b	14a	14b	15
Number of stations worked	20	9	4	4	3	3	3	3	3	3	1
Number of dredge hauls	66	22	12	16	7	9	8	6	4	3	1
Solaster papposus	0·41	0·32	0·17	0·38	0·14	–	–	–	–	–	–
Ophiura texturata	0·03	–	–	–	–	–	0·12	–	0·75	1·30	–
Buccinum undatum	2·32	2·95	0·67	1·44	0·86	4·44	3·62	3·00	2·00	4·00	3·0
Ostrea edulis	3·71	0·18	–	2·00	0·14	0·22	0·12	–	–	–	–
Eupagurus bernhardus	1·74	1·32	1·17	0·56	0·14	0·33	0·12	–	0·25	–	–
Macropodia rostrata	0·03	–	0·08	0·06	–	–	0·50	0·50	0·75	0·60	–
Hyas araneus	0·70	0·77	0·92	0·31	0·29	0·11	–	–	–	–	–

Table 15: *Upper Crouch, November* 1949
Mean numbers of epi-benthic animals per 50 *metre dredge haul*

Section	12a	12b	13b	14a	14b
Number of stations worked	7	4	7	3	3
Number of dredge hauls	18	10	21	7	6
Solaster papposus	0·11	0·10	–	–	–
Ophiura texturata	–	0·40	0·10	1·86	–
Buccinum undatum	1·67	0·20	–	1·86	0·17
Ostrea edulis	13·33	5·90	2·57	3·57	0·83
Eupagurus bernhardus	0·44	0·50	0·14	–	0·17
Macropodia rostrata	0·11	0·10	0·10	–	–
Hyas araneus	0·17	0·10	0·05	–	–

Table 16: *Upper Crouch, October* 1950
Mean numbers of epi-benthic animals per 50 *metre dredge haul*

Section	11b	12b	13b	14a	14b
Number of stations worked	3	3	3	3	1
Number of dredge hauls	8	5	8	6	3
Solaster papposus	0·50	0·20	–	–	–
Ophiura texturata	0·12	1·00	0·38	3·17	–
Buccinum undatum	2·00	2·80	4·75	4·33	1·67
Ostrea edulis	2·62	–	–	–	–
Eupagurus bernhardus	0·50	1·40	0·12	0·17	–
Macropodia rostrata	1·00	0·60	3·38	0·83	0·67
Hyas araneus	–	–	–	–	–

Table 17: *River Roach* 1950, *Mean numbers of epi-benthic animals per* 50 *metre dredge ha*

Section	4	5	6	7	8	9a	9b	10a
Number of stations worked	4	9	4	2	6	8	11	7
Number of dredge hauls	7	13	9	5	13	17	21	19
Solaster papposus	–	–	–	0·20	–	–	–	–
Ophiura texturata	0·14	–	–	0·20	0·08	0·18	0·10	–
Buccinum undatum	–	0·08	0·22	–	0·31	0·53	0·38	0·74
Urosalpinx cinerea	–	–	–	0·20	0·23	1·12	0·48	0·53
Ostrea edulis	0·14	0·15	2·89	0·20	8·85	5·29	5·76	0·89
Eupagurus bernhardus	–	0·15	0·33	1·60	0·77	0·18	0·10	–
Macropodia rostrata	–	–	–	–	–	–	–	–
Hyas araneus	0·43	0·23	0·11	0·40	0·31	0·18	–	–

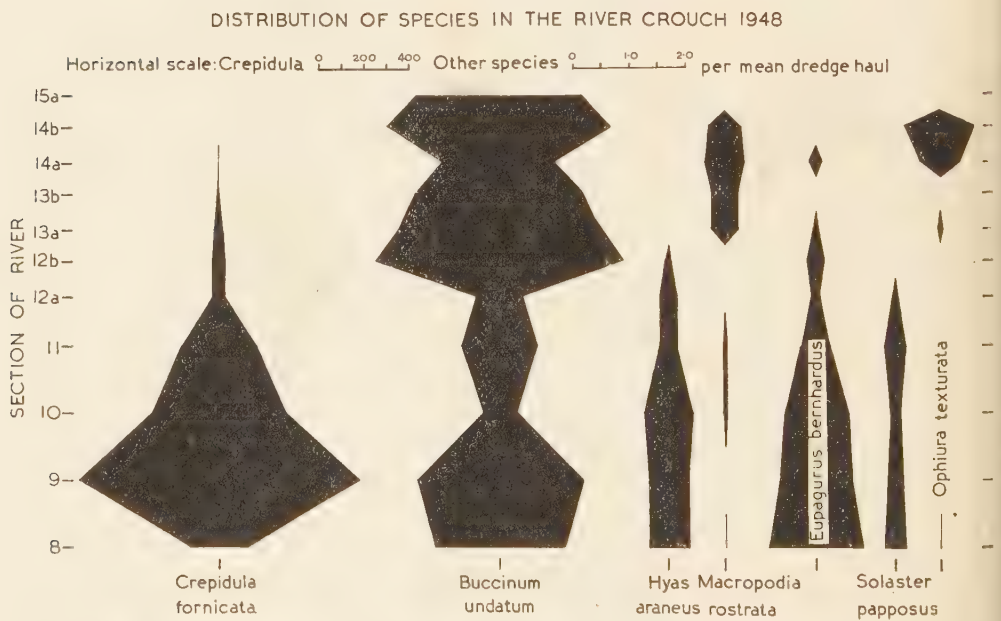


Fig. 30. *The abundance of the larger bottom invertebrates in Sections* 8 *to* 15 *of the estuary of the Crouch during the winter of* 1948-49.

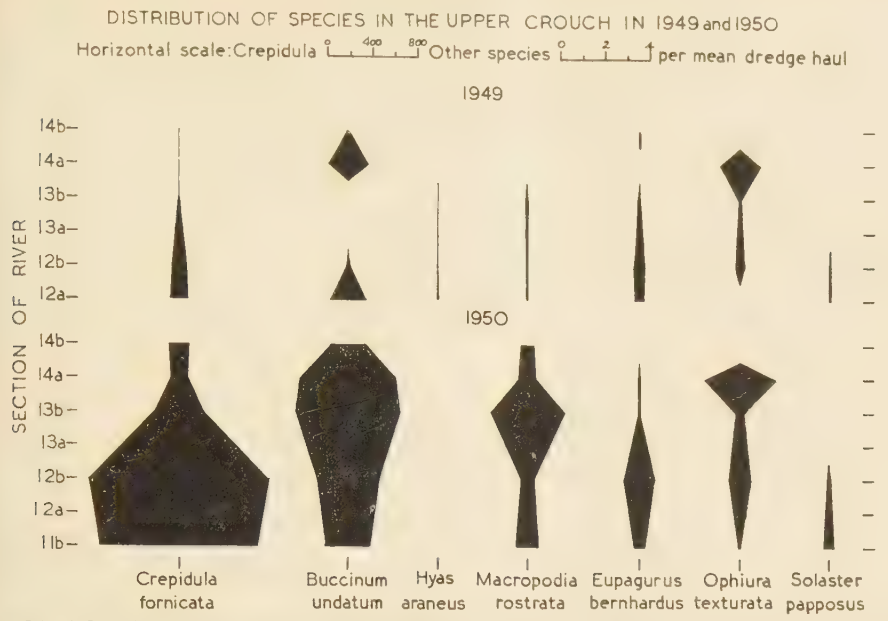


Fig. 31. *The abundance of the larger bottom invertebrates in the upper Crouch estuary in the winters of* 1949-50 *and* 1950-51.

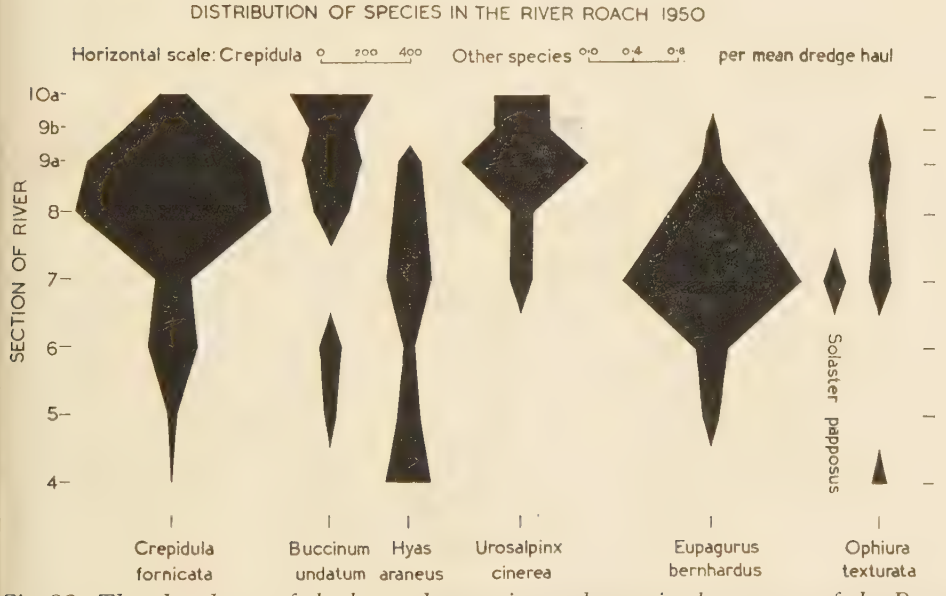


Fig. 32. *The abundance of the larger bottom invertebrates in the estuary of the Roach during the winter of* 1949-50.

ter papposus

. *papposus* is a northern form near the southern limit of its range (Mortensen, 1927); od comprises small molluscs and echinoderms (Allen, 1899, and Hunt, 1925).

lthough suitable food is apparently abundant, *Solaster* does not penetrate far up the ries of the rivers Crouch and Roach. Two factors may be of importance: lowered ty and the high temperatures which occur in shallow waters in the summer. It was ound in the muddy zone at the mouth of the river Roach.

Ophiura texturata

Mistakidis (1951) recorded a maximum of 1 to 2 per sq. metre in the Crouch and Roac *O. texturata* is probably omnivorous; Hunt (1925) found various polychaetes, crustac and lamellibranchs in its stomach, in addition to detritus.

O. texturata was discontinuously distributed in each of the two estuaries. Althou moderately common in some places outside the estuaries, e.g. in the Whittaker Chann where it grows to a rather larger size, it was rare in the lower estuary but commoner in t upper reaches. It is possible that flat fish and *Solaster*, which are known to feed on *Ophiu* (Hunt, 1925), are sufficiently abundant to keep it down, but do not penetrate into t shallow upper reaches where it can maintain a precarious hold. In the river Roach, *Ophiu* was present mainly in the upper reaches although in smaller numbers than in the Crouc

Buccinum undatum

This species is widespread in both estuaries.

Urosalpinx cinerea

This species, although widespread in the Roach, is rare in the upper Crouc An occasional specimen was found in Section 8 during the survey but none higher although it has since been recorded from Fambridge. Its absence from the upper Crou renders these grounds very favourable for the survival of oyster spat.

Although absent from the muddy lower reaches of the river Roach, *Urosalpinx* w present elsewhere in fair numbers up to Section 10a. Mistakidis (1951) recorded a maxim of 5 per sq. metre in Section 8, and notes that it prefers a bottom carrying a good deal shell or in a fair state of cultivation.

Buccinum and *Urosalpinx* are the two species, of those studied quantitatively, wh have the highest tolerance of estuarine conditions. This is probably correlated with t ability of both species to close their shells, by an operculum, when salinity is unfavoura reduced. It is clear that *U. cinerea* is liable to occur in all parts of estuaries suitable oyster culture.

Eupagurus bernhardus

Eupagurus is fairly tolerant of estuarine conditions and specimens were found o practically the whole area surveyed: few were, however, found on the soft mud at mouth of the Roach.

Macropodia rostrata

This species was not found in the river Roach. In the Crouch it was rare in the lo reaches, but it was more abundant in the upper estuary. It favours grounds on wh branched hydroids occur (Allen, 1899). In the Crouch there is a considerable growth sponges, hydroids, (especially *Sertularia cupressina*) and seaweeds in the shallow u reaches. This may explain the higher density of *Macropodia* but it does not explain absence from the Roach where the water is less turbid than in the lower Crouch, (Mistaki 1951), and sponges and hydroids are as prolific as in the upper Crouch.

The density of *M. rostrata* increased during the period 1948-1950 in the upper reac of the river Crouch. In the autumn of 1950 small juveniles were very common but t were not included in the quantitative data as many must have escaped through the mes of the dredge.

Hyas araneus

H. araneus has a poor toleration for estuarine conditions. In the river Crouch only occasional specimen was found above Section 12a. In the river Roach its distribution v similar extending only a little beyond that of *Solaster papposus*. Of the nine species studi this spider crab was the most tolerant of the soft mud in the lower reaches of the Roach.

A few notes on species which are small enough to escape through the meshes of dredge are given below.

Nassarius reticulatus (See Mistakidis, 1951)

N. reticulatus is generally common on Essex oyster grounds and locally very abunda In the Crouch it penetrated into Section 12b and in the Roach into Section 9b.

dium exiguum

This species is very common and was found on all types of bottom except pure mud. he Crouch it extends into Section 15a and in the Roach into Section 10a. As these rds show, *C. exiguum* is very tolerant of low salinity. Mistakidis (1951) recorded a imum of 6 per sq. metre in the Crouch (Section 5) and 15 per sq. metre in the Roach tion 8).

cinus moenas

The green crab was common throughout the area studied. Below low water mark, it is e abundant in the creeks and shallow upper reaches than in the lower estuary.

cellana longicornis

This is a very common species which is tolerant of estuarine conditions. It extended Section 14b in the Crouch and Section 9b in the Roach. *Porcellannaplatycheles* seems e absent from the rivers Crouch and Roach.

erias rubens

In this survey starfish were not found higher than Section 12a in the Crouch. *ubens* seems to require more open water conditions and is common off the mouth of the rs Blackwater and Colne, where perhaps it is also favoured by the reduced scale of the perature and salinity fluctuations.

5. COMPARATIVE OBSERVATIONS ELSEWHERE IN ESSEX

ME general surveys were made of other parts of the Essex coast and the distribution *. fornicata* and the other major invertebrates recorded. For convenience the dredge

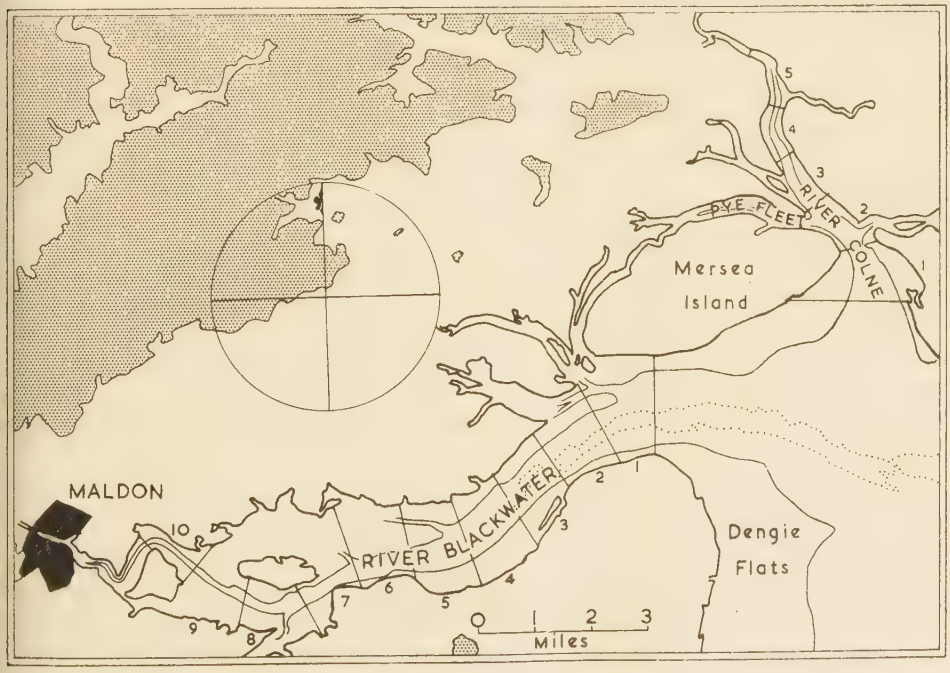


Fig. 33. *The estuaries of the rivers Blackwater and Colne, the sections into which they were divided, and the surrounding topography. The land over* 30·5 *m.* (100 *ft.*) *above sea level is stippled. The* 5 *fathom* (9·1 *m.*) *depth contour is shown as a dotted line.*

hauls have been grouped into those made, (a) offshore, beyond the mouth of the rive (b) in the river Blackwater and (c) in the river Colne. The rivers Blackwater and Col have been divided into sections 1600 m. in length (Fig. 33). Table 18 records the observ presence or absence of various species in the three areas studied.

Table 18: *Distribution of the larger epi-benthic invertebrates. Stations where pres indicated thus* +

Area	Off-shore survey	River Blackwater Survay (March 1950)											River Colne Survay (March 1950)				
Section		1	2	3	4	5	6	7	8	9	10a	10b	1	2	3	4	
Number of dredge hauls	28	2	2	7	3	5	3	2	2	3	2	1	6	2	6	2	
Solaster papposus	+				+	+		+									
Asterias rubens	+												+				
Buccinum undatum	+			+		+	+			+							
Urosalpinx cinerea						+	+										
Crepidula fornicata	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	
Ostrea edulis		+	+	+	+	+	+	+	+	+	+		+	+	+		
Eupagurus bernhardus	+			+			+						+				
Hyas araneus				+	+	+	+	+					+	+			

(a) *Offshore*

Dredge hauls were made in February 1949 in the Whittaker Channel outside mouth of the Crouch, as far seaward as the South Buxey buoy. *C. fornicata* was found in parts of the channel examined although in small numbers, not more than 20 per h The bottom was generally sandy with broken shell. Aggregations of *Sabellaria* w common. *Crepidula* was also general in hauls made outside the mouth of the Blackwat Colne river systems. A distinctive feature of this area was the great abundance of *Aster rubens*; in two hauls made at a depth of 12 metres outside the Blackwater, 128 individu were caught.

(b) *River Blackwater*

This is a large tidal inlet with a comparatively small volume of fresh water enter at the head of the estuary. Estuarine conditions do not persist to the same extent as in river Crouch, the more marine forms dying out only above Section 7. *C. fornicata* widespread and often abundant; large numbers were caught in the dredge in parts Sections 3, 4, 7, 8 and 9. Grab samples (Table 10) taken in Section 3 gave a maxim density of 594 per sq. metre. The estuary shallows rapidly above Section 7 and Section 10b there is less than a metre depth at low water. The conditions then clos resemble those at Brandy Hole in the river Crouch and slipper limpets do not pers In Section 10b, neither live specimens nor empty shells were found.

River Colne

The Colne is the smallest of the four estuaries examined and estuarine conditions are current from Section 3 upwards. In the upper part of Section 4 and in all of Section 5 depth at low water is about 2 m. In Section 4 there were moderate numbers of *fornicata* but none were found in Section 5 nor were any empty shells seen. In Pyefleet few were found; in this channel *Paphia pullastra* was unusually common.

In the lower reaches of the estuary, *C. fornicata* although common, was less abundant than in the other four estuaries. It is possible that the steady efforts of the Colne Fishery Board, in this comparatively small area, have been sufficient to keep it under control.

Discussion

This paper is intended as a contribution to the understanding of the biology of an important pest of the east coast oyster beds of England. This pest is steadily spreading and now found on nearly all important oyster grounds on the English coast.

From the laboratory experiments and the results of the field surveys recorded in this paper, it is clear that *C. fornicata* is likely to flourish on all oyster grounds. Indeed, the abundance of the American slipper limpet forms a very good guide to the hydrographic possibility of an area for oyster culture, since the estuarine requirements of the two species are very similar.

Slipper limpets take four or five years to reach full size and most individuals probably live for eight or nine years. The annual spatfall varies in a similar manner to that of oysters and is likely to be more intense where the population is dense than in areas where the pest is comparatively scarce. From these facts it is evident that grounds which are regularly and thoroughly cultivated are unlikely to be greatly troubled by this pest since much of the bottom material will be brought to the surface every few years and any small chains will be removed. However, when grounds have been derelict for a number of years, as during the war, or when the fishing effort is spread too thinly over a large area, severe trouble may be experienced.

Although it has not been conclusively demonstrated that large populations of slipper limpets are harmful to oysters, it is natural to assume that the great abundance of an organism, whose adult and larval stages have similar feeding methods to oysters, is serious to the maintenance of large oyster populations. In this connection calculations of the numbers of slipper limpets in certain stretches of the Essex rivers are of interest. Orton (1951) made a detailed survey of two derelict grounds, one in the Crouch and the other in the Roach. On these two grounds 446 and 179 slipper limpets were found respectively on an average square metre (1·2 sq. yds.) of bottom. In the survey recorded in Part IV of this paper, 50 dredge stations were worked in Sections 8-12 of the Crouch. The total area of these five Sections is about 2·15 sq. kilometres (531 acres). Assuming 50 per cent efficiency for the oyster dredge used (see p. 34), the average density for all stations in these Sections was 76·2 limpets per sq. metre of bottom. Thus in these 8 kms. (5 miles) of the river Crouch there were about 165 million individuals or 1,150,000 kilos (1,129 tons).

Thus slipper limpets far exceed oysters in abundance and to improve substantially the conditions of the river in favour of the oyster, *Crepidula* must be removed. Undoubtedly the best method of doing this is by the efficient use of mechanically operated gear. For such purposes dredges which were originally designed for hand operation in sailing boats are unsuitable.

The question of limpet disposal when caught is pertinent; the decks of boats quickly become blocked when working on infested ground. A commercial outlet would, of course, be attractive. If no commercial outlet is available, there are three methods by which dredged slipper limpets can be destroyed. The common practice is to deposit them as high on the shore as can conveniently be reached. This is effective if they are dumped well up

the shore as sooner or later they die in this position. Usually, however, they are shovell overboard when the boat is as near inshore as it can get when the tide is high and occasion limpets are discharged low down on the beach where they will live for a long tim

A small crusher, driven by a belt from the engine, has been installed on the Ministry smack 'WYSTRYS' at Burnham-on-Crouch. The crushed slipper limpets are thrown ove board, thus keeping the decks clear. This method of disposal has the advantage that t slipper limpets are continuously dealt with as dredging proceeds. A disadvantage is th they have to be roughly sorted before crushing, as stones, to which the clusters are oft attached, tend to jam the crusher or to break the teeth.

Korringa (1951b) has shown that if the mixture of shell cultch, young slipper limpe and young oysters, that is brought up in a dredge, is left overnight in a dilute solution mercuric chloride or copper sulphate, the slipper limpets are killed but not the oyste This procedure, however, involves much handling of the dredge material and requir quays where the boats can discharge at all states of the tide. It is considered that th technique would be of value in Britain in the final stages of extermination of the p once the majority had been removed from the rivers by the normal sorting of the dredg material.

Summary

1. An investigation was made of the influence of temperature and salinity on the Americ Slipper Limpet, *Crepidula fornicata*. The growth rate was studied in detail in the ri Crouch and the distribution of *C. fornicata* and the other principal epi-benthic forms w recorded in the rivers Crouch, Roach, Blackwater and Colne.

2. Laboratory and field experiments showed that the activity of the feeding current w influenced by temperature and salinity. Field observations showed that at temperatu below 5° C. few slipper limpets were feeding. Although laboratory experiments showed th a salinity of 25‰ markedly reduced the feeding current, no mortality occurred when slip limpets were kept at this salinity for two months. Adults were not killed when kept in t air at — 4°C. to — 6°C. for less than 4 hours.

3. An account is given of the weight, the proportions of the shell, and the weight of me at different sizes.

4. The growth rate was observed by measuring the shell length of a number of samp taken over a period of 2½ years from one station in the river Crouch. The modes different year-classes could be distinguished in size-frequency curves at sizes below 3 c Above this size the year-classes were closely overlapped. During the first winter the mo size varied from 4 to 8 mm.; during the second, from 12 to 14 mm. The modal size in t third winter was only distinguishable for one-year class (1950), of which the mode w at 18 mm. while the range was 12 to 28 mm. Extrapolation of the growth curves suggest that most individuals at this station do not reach a size of 4 cm. until the 6th summer.

5. An examination of the position in the chain of individuals below 3 cm. confirms Orto hypothesis that, on the average, one individual is added to the main chain each ye An examination of the position of larger individuals confirms the estimation of age made extrapolating the growth rate.

6. Shell growth occurred from March to September. Growth started when the wa temperature exceeded about 8 C. but stopped in the autumn when, although falling, t temperature was still about 15°C. About half the annual growth was made in the t months, June and July.

7. The time and intensity of spawning was recorded from one station in the river Crou for three successive summers. The proportion of 0-group slipper limpets has been record from various sections of the river Crouch in 7 consecutive winters (1947-48 to 1953-5 The average for the whole estuary in one winter has varied from 3·4 to 50·4 per ce

mean for the 7 winters was 19·0 per cent. The proportion of 0-group slipper limpets ne winter was directly correlated with the proportion of oyster larvae which grew to the of metamorphosis in the preceding summer, indicating dependence upon similar ronmental factors.

he bottom soil, depth and hydrography of the estuaries of the rivers Crouch and Roach briefly described.

he abundance of *Crepidula fornicata* in part of the river Crouch and all of the river ch was determined by dredging. *C. fornicata* thrives wherever oysters can be vated.

The abundance of *Solaster papposus*, *Ophiura texturata*, *Buccinum undatum*, *Urosalpinx rea*, *Eupagurus bernhardus*, *Macropodia rostata*, *Hyas araneus* and *Ostrea edulis* is ribed.

The results of a general survey of the distribution of *C. fornicata* and the other large benthic forms made in the rivers Blackwater and Colne, are outlined.

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